AD-A054 638 NAVAL RESEARCH LAB WASHINGTON D C F/G 8/1
THE OCCURRENCE AND DISTRIBUTION OF SURFACE BIOLUMINESCENCE IN T--ETC(U)
APR 78 R V LYNCH

UNCLASSIFIED NRL-8210 SBIE-AD-E000 159 NL

| OF |
AD
A054638

END
DATE
FILMED
6-78
DDC

NRL Report 8210

The Occurrence and Distribution of Surface Bioluminescence in the Oceans During 1966 Through 1977

RICHARD V. LYNCH III

Marine Biology and Biochemistry Branch
Ocean Sciences Division

April 26, 1978

NAVAL RESEARCH LABORATORY
Washington, D.C.

(18) SBIE (19) AD-E000 259

SECURITY CLASSIFICATION OF THIS PAGE (When Data Entered)

REPORT DOCUMENTATION PAGE	READ INSTRUCTIONS BEFORE COMPLETING FORM
1. REPORT NUMBER: NRL Report 8210 (14) NRL-8210	2. GOVT ACCESSION NO. / 3. RECIPIENT'S CATALOG NUMBER
4. TITLE (and Subtitle): (6) THE OCCURRENCE AND DISTRIBUTION OF SURFACE BIOLUMINESCENCE IN THE OCEANS DURING 1966 THROUGH 1977	5. TYPE OF REPORT & PERIOD COVERED: (9) Interim report
	6. PERFORMING ORG. REPORT NUMBER
7. AUTHOR(s): (10) Richard V. Lynch III	8. CONTRACT OR GRANT NUMBER(s): (11) 26 Apr 78
9. PERFORMING ORGANIZATION NAME AND ADDRESS: Naval Research Laboratory ✓ Washington, DC 20375	10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS: NRL Problem 86 G04-04
11. CONTROLLING OFFICE NAME AND ADDRESS: Office of Naval Research Arlington, VA 22217	12. REPORT DATE: April 26, 1978 (12) 49p. / 13. NUMBER OF PAGES: 48
14. MONITORING AGENCY NAME & ADDRESS (if different from Controlling Office)	15. SECURITY CLASS. (of this report): Unclassified / 15a. DECLASSIFICATION/DOWNGRADING SCHEDULE

16. DISTRIBUTION STATEMENT (of this Report)

Approved for public release; distribution unlimited

17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)

18. SUPPLEMENTARY NOTES

19. KEY WORDS (Continue on reverse side if necessary and identify by block number)

Bioluminescence
Copepods
Dinoflagellates
Euphausiids

20. ABSTRACT (Continue on reverse side if necessary and identify by block number)

Displays of bioluminescence, caused by many different organisms, occur throughout the oceans of the world. Some of these are spontaneous; others can be attributed to a known stimulus, such as the turbulence caused by the passage of a fish school or ship. Moreover, low light level image intensifiers enable us to see displays invisible to the unaided human eye. The last surveys of the occurrence of bioluminescence in the oceans were made in 1966. This report brings those surveys up to date. In addition, the results of five NRL cruises are presented. On those cruises, bioluminescence was found

(continued on back)

DD FORM 1 JAN 73 1473 EDITION OF 1 NOV 65 IS OBSOLETE S/N 0102-014-6601

SECURITY CLASSIFICATION OF THIS PAGE (When Data Entered)

251 950

20. ABSTRACT (continued)

CONT

almost everywhere along the cruise tracks. The principal causative organisms were identified as euphausiid shrimp, dinoflagellates, and copepods. Salps, coelenterates and ctenophores, and ostracod crustaceans were responsible for luminescence in certain limited areas.

ABSTRACT

CONTENTS

OCCURRENCE AND DISTRIBUTION OF SURFACE BIOLUMINESCENCE IN THE OCEANS DURING 1966 THROUGH 1977

INTRODUCTION

Bioluminescence is the emission of light by living organisms. Although the best known example is the firefly, many other creatures also luminesce. These are found on land, in fresh water, or in salt water, but the greatest number and diversity are found in salt water. It has been estimated that in the deep ocean, where sunlight never penetrates, possibly 70% of the species and 90% of the individuals are luminous. Luminescence in the sea is not confined to the depths, for not only do some luminous species migrate to near the surface at night, but there are also many other luminous species living near the surface or in shallow water.

When luminescent organisms congregate near the surface in sufficiently large numbers, luminous displays occur. These displays can be classified into several categories according to their appearance. First is *white water* or *milky seas*, in which a large area of ocean, frequently from horizon to horizon, appears as a sheet of steadily glowing light. Smaller patches of ocean may also appear to be luminous. These patches may seem to contract and expand, to glow steadily, or to glow intermittently. Sometimes they seem to travel at high speeds until out of sight. Finally, large areas of ocean may sparkle with rapidly scintillating point sources of light. These types of displays occur without apparent stimulation of luminescence on the part of the observer.

Luminous displays of the above character are sufficiently striking and uncommon that when they are observed they are usually reported. Rarer and even more spectacular displays exist, however. One of these is undulating waves of light, in which rapidly moving bands of light alternating with bands of darkness appear to travel from horizon to horizon. A second rare display is the *phosphorescent wheel*, in which alternating arms of light and darkness appear to rotate around a central point, similar to a fireworks pinwheel. Sometimes several wheels can be seen simultaneously. Finally *bubbles* of luminescence occasionally are seen. These are balls of light which appear to rise from the depths and burst against the sea surface.

In spite of the spectacular nature of these bioluminescence displays, in no case are the causes known. No chemical or physical studies of the sea water or atmosphere at the surface have been made during a display. Few organisms have been collected during one. Most of the observations have been made by seamen or travellers, not scientists. Many of the observers have been members of the U.S. Navy. These observations, along with other widespread reports, have created a long-standing interest in bioluminescence in the Navy. Furthermore, the Navy's interest goes beyond displays. A luminous display can occur only

Manuscript submitted February 8, 1978.

where there is a sufficiently large concentration of luminous organisms to emit light visible to the naked eye. Such large concentrations are uncommon. However, luminous organisms are common in the ocean and, when disturbed, will emit light that can be detected using instruments. The most common instruments used for this purpose are bathyphotometers and low light level image intensifiers (LLLII's).

Bathyphotometers are of two kinds: passive and active. Passive bathyphotometers consist of one or more photocells exposed unshielded to the ocean. They record any spontaneous bioluminescence within their field of view, and also any other light in the water, such as sunlight or moonlight penetrating from above. An active bathyphotometer consists of a photocell looking into an enclosed, shielded chamber. Sea water containing organisms is pumped into the chamber, and the turbulence so generated stimulates any luminous organisms present to flash or glow. This active process is advantageous in that it does not record extraneous light, but disadvantageous in that only small weak-swimming organisms pass into the chamber. Neither kind of bathyphotometer, by itself, can be used to identify the bioluminescent organisms whose light they record.

LLLII's are among the newest tools for detecting bioluminescence in the field. Developed from the *Starlight Scope* first used in Vietnam, their technology has been improved in less than a decade until now they can enhance light intensity by up to a factor of 100,000. A LLLII customarily consists of a closed-circuit television camera and lens, a TV monitor, and a video tape recorder. The TV camera includes an image-intensification tube. The greatest enhancement can currently be achieved using a modified silicon intensified-target tube called an ISIT. Earlier models used an ordinary camera coupled to a starlight scope, or a secondary electron conduction (SEC) vidicon tube. A LLLII system of this nature is described by Roithmayr (1970) and Roithmayr and Wittmann (1972). This system has been mounted in an airplane and used to detect schools of commercial fish moving through areas containing luminous plankton in the Gulf of Mexico, the Gulf of Maine, off the coast of Southern California, and near Aberdeen, Scotland (F. Wittmann, personal communication). Results of these tests and pictures of fish schools taken at night are presented in Roithmayr (1970), (1971), Drennan (1969), (1971), and Stevenson (1975). In addition, an identical system has been used off the coast of Southwest Africa to detect fish schools for commercial fishermen. These results can be seen in Cram (1972), (1973), (1974), and Cram and Hampton (1976).

Luminous marine organisms have achieved varying degrees of control over their luminescence. At one end of the scale are luminous bacteria, which have no control over their luminescence and which glow continuously. At the other end are fish and squids, which have achieved nearly complete purposeful control. In between are most of the luminous planktonic organisms, which automatically respond to certain kinds of external stimulation by luminescing. In the laboratory, many luminous marine organisms can be stimulated to emit light by chemical, electrical, mechanical, or photic means. At sea, luminous displays are most commonly stimulated mechanically or photically. Ships moving through water containing luminous organisms are a frequent cause of mechanically stimulated displays. The turbulence caused by the ship's passage causes glowing bow waves and wakes. The glowing wakes often extend a distance equal to several times the ship's length. Rough surface conditions and moving schools of fish are other common causes of mechanically stimulated displays. Photically stimulated displays can be triggered by shining a lantern or flashlight briefly into the water. When this is done large areas of water often flash in response. Furthermore, if organisms in one area are mechanically disturbed until they flash, organisms

outside the area of initial disturbance frequently flash in response to that light, thereby greatly extending the luminescent area.

Congregations of luminous organisms occur more frequently in some places and seasons than in others. However, there have been few systematic studies of this variability. The distribution and occurrence of luminous displays have been discussed by several authors: [Kalle (1960), Staples (1966), Turner (1965), (1966), Verploegh (1968)]. Since 1966 our knowledge of the biology, physiology and biochemistry of various species of luminous marine organisms has grown considerably. Some of these advances, along with several recent observations of displays, are outlined by Herring (1976b). This report attempts to update the reports of Staples and Turner, to map reports of the occurrence of luminous organisms in areas where no displays have been reported, and to present data gathered on five cruises by the Naval Research Laboratory on the distribution and occurrence of luminescence in the ocean.

MATERIALS AND METHODS

The data in this paper on the occurrence and distribution of bioluminescence at sea since 1966 are presented as points on a series of maps. Each point represents at least one observation at that geographic location. An observation is considered to be either the sighting of luminescence in the water by eye or by a LLLII, the detection of bioluminescence near the surface by a bathyphotometer lowered into the water, or the catching and identification of known luminous organisms by plankton tows.

The majority of observations were gleaned from a literature search of papers published during or after 1966. While it is impossible to acknowledge each observation plotted on the map, every paper from which an observation was taken is listed in the bibliography. An attempt has been made to present the data seasonally. Any reports too vague to allow determination of the season have been omitted, with the exception of Indian Ocean reports for the northeast monsoon. Reports of luminescence during the northeast monsoon have been arbitrarily placed during January or February, unless the exact date was mentioned, even though the monsoon period covers December as well. Reports of luminescence attributed to fish, cephalopods, and benthic organisms have been deliberately omitted on the grounds that these organisms do not contribute to displays of the type to be detected using a LLLII. Two exceptions are hereby noted. The squid *Watasenia scintillans* at certain times of the year appears off the north coast of Honshu, Japan, in large enough numbers to cause displays. Second, the teleost fish *Photoblepharon* and *Anomalops* found in the Red Sea, Indian Ocean, and South Pacific, school near the surface and create displays. Displays due to these three organisms have been mapped.

Colonies of luminous bacteria have been isolated from sea water from many locations and grown on plates. Luminous bacteria have long been suspected of causing displays, especially when the light glows steadily. However, no display has been specifically shown to be due to luminous bacteria. In spite of the widespread occurrence of luminous bacteria in the ocean, and the suspicion that they cause displays, no locations at which only luminous bacteria were reported have been included on the maps. It has been shown [Nealson, Platt and Hastings (1970), Nealson, Eberhard and Hastings (1972), Eberhard (1972)] that luminous bacteria release into their surroundings a substance that induces the synthesis of luciferase. Fairly high concentrations are necessary to induce synthesis. When the

concentration of this unknown substance is too low, no luciferase is synthesized and the bacterial cell maintains only a barely detectable glow. In the open sea, the concentration of luminous bacteria is too low to maintain a sufficiently high concentration of inducer molecule to permit luciferase synthesis. Consequently, in the open sea one would not expect luminescence due to luminous bacteria.

Some of the observations plotted here have not appeared in the literature. These have been personally reported to the author by reliable observers. In all such cases, the visual description provided was verified to ascertain that bioluminescence was seen and not reflected light or iridescence. In many of these cases the observation was substantiated by examination of captured luminous organisms or a portion of a recording from a bathyphotometer.

Finally, the author made bioluminescence observations on five cruises for the Naval Research Laboratory aboard the R/V MIZAR or R/V HAYES. The tracks of these cruises are shown on the maps. The tracks have been fortuitous, not planned to give a systematic survey or to study waters with known high occurrences of bioluminescence. Surface plankton tows were made twice a night, approximately one hour after sunset and two hours before sunrise along the cruise track, using a 50-cm plankton net with 35-micron mesh pore size. Tows were carried out for 15 minutes at a speed of two knots. Altogether 169 tows were made and examined for the presence of luminous organisms. In only one of these tows was no luminescence found.

Portions of the plankton catches were placed in a photometer [designed and built by Mitchell and Hastings (1971)] in a darkroom on board ship and their spontaneous flashing recorded using a Hewlett-Packard 7101 BM high-speed strip-chart recorder. Flashes were bright and numerous, although it must be pointed out that many organisms were probably excited or injured in the process of collection. A typical pattern is shown in Fig. 1. Some catches contained so much luminescence that it was almost possible to read by them.

Bathyphotometer lowerings were made to as deep as 200m at several points on three of the cruises. The bathyphotometer used was a pressurized version of the one designed by Seliger, et al. (1962), with a modified pump and connected to a Sanborn Model 299 high-speed strip-chart recorder. Luminescence was recorded on every lowering, with the greatest number of flashes occurring near the surface. Typical flash patterns at various depths are shown in Fig. 2.

Several maps show a low incidence of luminescence. This dearth does not necessarily mean that luminescence in these areas was lacking, but only that no observers were present or made a report. For comparison, the maps prepared by Staples (1966) are herein reproduced.

RESULTS

Atlantic Ocean and Related Seas (Figs. 3 through 7)

Luminous organisms of all groups were collected throughout this region in the past decade. Euphausiids and dinoflagellates were especially abundant. Luminous dinoflagellates were observed in large numbers in the Gulf of Mexico, the South Atlantic off the coast

of Brazil, the Caribbean and the Barents Seas, and along the coasts of the United States, western Scotland, Norway, and the Crimean peninsula. Along the Texas, west Florida, Maine, Scotland, and Norway coasts, various species of luminous dinoflagellates were the major organisms in red tides. In Oyster Bay near Falmouth, Jamaica, and Bahia Phosphorescente and Puerto Mosquito, Puerto Rico, luminous dinoflagellates were found permanently in large concentrations. Thus, these three bays have often been called "luminous bays." In the late 1960's and early 1970's, the dinoflagellate population of Oyster Bay underwent a catastrophic decrease. The causes of this decrease are unknown but are probably related to man-made disturbances on shore. Although for several years it was thought that the bay had "died," the author observed high levels of luminescence in Oyster Bay in 1976, and was then informed that luminescence appeared to be returning slowly. Seasonally, dinoflagellates have been collected all year around and red tides generally have occurred in late spring and early autumn.

Like dinoflagellates, euphausiids have been collected from almost all of the areas shown in the maps. They were especially common in the Barents Sea and off the west coast of Scotland, and were somewhat sparse in the Mediterranean and near Iceland. In the author's collections, euphausiids occur more frequently than do dinoflagellates.

Other luminous organisms have appeared locally in large numbers. The Barents Sea has been reported rich in luminous copepods, and the author found them abundant in the western Mediterranean as well. The salp *Pyrosoma* is common in the eastern Mediterranean. In the heavily oil-polluted waters along the coast of Venezuela and around Trinidad, most of the plankton taken from the author's nets were dead. One of the few surviving organisms was a luminous shrimp of the genus *Lucifer*. Luminous coelenterates have been sporadically collected.

Pacific Ocean and Adjacent Seas (Figs. 8 through 13)

In the past decade too few observations of bioluminescence were made to establish any kind of distributional pattern for luminous organisms in the Pacific area. As in the Atlantic, luminous dinoflagellates were widespread, being among the most common dinoflagellates in the red tides near Los Angeles and on the Inland Sea of Japan. The author observed luminous dinoflagellate blooms near Madang, Papua New Guinea, and collected large numbers of them off the Pacific coast of Central America and northeast of Hawaii. Likewise, euphausiids were widely distributed. These were reported abundant off the coast of central California, and the author collected them all along the route on cruises from Japan to American Samoa via Papua New Guinea, and from Panama to Hawaii. They were especially abundant off the coast of Panama and near Papua New Guinea. Luminous ostracods were abundant near Tokyo Bay, Japan, Palau and Yap Islands, and Madang, Papua New Guinea. The author collected abundant luminous ctenophores south of Honshu and in the Solomon Sea. The squid *Watasenia scintillans* created displays on the north coast of Honshu.

Indian Ocean (Figs. 14 and 15)

The International Indian Ocean Expedition provided data on that area during the period from 1959 to 1965. The scientists involved were not primarily concerned with bioluminescence, but an analysis of known luminous species from their distributional reports

for various planktonic groups has shown luminous organisms to occur throughout. As expected, luminous dinoflagellates and euphausiids were the most widespread and numerous. Luminous copepods were also widely distributed, while luminous salps commonly occurred around South Africa and chaetognaths in the Arabian Sea.

Plankton Tows on NRL Cruises

Out of 169 tows, bioluminescence was found in all but one. The exception was a tow made between Iceland and Greenland in August, when the night was only a few hours long. In the remaining samples, euphausiid shrimp, dinoflagellates, and copepods were the most common luminous organisms found. A partial analysis of the frequency of occurrence of common luminous organisms found is shown in Fig. 16. The random nature of the cruise tracks indicates that we might expect to find one or more of these luminous organisms at or near the surface practically everywhere in the sea.

DISCUSSION

Naval Interest

Naval interest in bioluminescence centers around its use as a tool for detecting moving objects at night. If we were confined to using only luminescence visible to the human eye for this purpose, its usefulness would be very limited. However, luminescence invisible to the human eye can be detected using a LLLII. Even LLLII's have limits, as in the case where moonlight reflected from the sea surface tends to mask bioluminescence by decreasing the contrast between the luminescent area and the background. A promising approach to lessening the influence of moonlight and also to lowering the limit of detectability is to use a digital image memory processor in connection with the LLLII. The capabilities of this method are described by Mengers (1977). Even the best detectors finally encounter the limits posed by the biologies of the various luminous organisms, the physical characteristics of the emitted light, and the biochemistry of their luminescent reactions.

Biological and Physiological Characteristics

Two factors determine the potential visibility of an object in luminescent waters: the concentration of organisms present and the intensity of their emitted light. A given concentration of a bright organism might create an easily visible display, whereas an equal concentration of a dimmer organism might be seen only with difficulty, if at all. Our ability to use marine bioluminescence as a detection method thus depends on knowing the distribution of various luminescent organisms. Unfortunately, our knowledge of this area is inadequate, for there have been few scientific cruises measuring luminescence in the ocean and collecting luminous organisms. Most observations of luminescence at sea do not identify the organisms present. Seasonal and depth distributions also require study, for luminous organisms are known to migrate vertically and seasonally, and to increase in numbers during certain seasons.

Also important in determining the brightness of a display is the intensity of the stimulus. Some organisms respond to a stimulus with a flash of maximum intensity, provided

that the stimulus is greater than some minimum threshold value which differs for different species. Other organisms grade the intensity of their response to the intensity of the stimulus. In either case, repeated stimuli cause repeated responses until fatigue sets in, after which no response is given to any stimulus until time has been provided for recovery. As fatigue gradually sets in, subsequent responses diminish in intensity compared to earlier responses. The rapidity of this intensity decrease, the number of responses before fatigue occurs, and the length of time needed for recovery differ for various species.

Finally, whether or not an organism responds to photic stimulation is important in determining the area of response. An organism which gives a luminous response to flashes of light creates an area of display considerably larger than the area of disturbance, because organisms near the area of disturbance, even though undisturbed themselves, respond to the light emitted by the disturbed organisms and, in turn, trigger those still further away to emit also. The visibility of a display depends on its area. Among the organisms that respond to photic stimulation are ostracods, dinoflagellates, coelenterates, ctenophores, and salps.

Physical Characteristics

It was shown above that the intensity of light emitted by an organism is important in determining the visibility of a display. Table 1 lists the intensities of emitted light for many of the known luminous marine organisms. Unfortunately, these intensities were measured by different observers and expressed in a variety of units. No attempt is here made to transform all intensities into a common set of units. Even so, one can see that the range of intensities is large. Table 1 also shows the emission wavelengths of many species; as can be seen, most luminous marine organisms emit light in the blue-green region. This means that an image intensifier maximizes light enhancement and minimizes noise if it employs a phototube with a peak response in this region. Gating could also be used to eliminate wavelengths outside the range of interest. However, since the identity of the luminous organisms present in a given area is not always known, a narrow gate could create a sampling bias.

Comprehension and Reliability of the Maps

Previous studies have looked primarily at visible displays of bioluminescence in the ocean. This report is concerned not only with visible displays, but also with the general distribution of luminous organisms. The development of LLLII's, which extend our ability to detect luminous displays invisible to the unaided human eye, makes this approach valid. Thus, while this report is more comprehensive than previous ones, it covers a much smaller time span—only from 1966 to the present—while earlier reports covered all observations up to 1966.

This report shares one bias with earlier reports. That is, most of the observations shown depended on the casual presence of an observer. Consequently, infrequently travelled areas show few or no observations, while heavily travelled regions show many. Therefore the number of observations in a given area cannot be taken as an indication of the relative frequency of occurrence at that location, nor can the maps be used to extrapolate or predict occurrences.

TABLE 1

Group	Species	Peak wavelength, nm	Intensity	Reference
Bacteria	—	470–500	10^4 quanta s^{-1} per cell	Nicol, 1962
Dinoflagellates	Polykrikos schwartzii	480	7.8×10^{-9} W per cell	Tett, 1969a
	Gonyaulax polyedra	480	2.3×10^9 quanta s^{-1} per cell	Seliger, Biggley & Swift, 1969
	G. catenata	480	1.2×10^{-9} W per cell	Tett, 1969a
	Pyrodinium bahamense	480	5.6×10^9 quanta s^{-1} per cell	Seliger, Biggley & Swift, 1969
	Peridinium depressum	480	7.8×10^{-9} W per cell	Tett, 1969a
	P. divergens	480	13.2×10^{-9} W per cell	Tett, 1969a
	P. ovatum	480	3.6×10^{-9} W per cell	Tett, 1969a
	P. pallidum	480	5.6×10^{-9} W per cell	Tett, 1969a
	P. steinii	480	3.4×10^{-9} W per cell	Tett, 1969a
	Dissodinium (Pyrocystis) lunula	480	8.0×10^{10} quanta s^{-1} per cell	Seliger, Biggley & Swift, 1969
	Noctiluca scintillans (miliaris)	480	2.1×10^{-7} W per cell	Eckert, 1966
	Pyrocystis acuta	474	1.1×10^{10} quanta s^{-1} per cell	Swift, Biggley & Seliger, 1973
	P. fusiformis	474	1.2×10^{11} quanta s^{-1} per cell	Swift, Biggley & Seliger, 1973
	P. notiluca	474	1.8×10^{11} quanta s^{-1} per cell	Swift, Biggley & Seliger, 1973
Radiolaria	Cytocladus major and Aulosphaera triodon	—	5.3×10^{-11} Wm^{-2} at 1 m	Nicol, 1958c
Hydrozoa	Colobonema sericeum	—	9.5×10^{-11} Wm^{-2} at 1 m	Nicol, 1958c
	Crossota alba	—	0.4×10^{-11} Wm^{-2} at 1 m	Nicol, 1958c
	Aeginura grimaldii	—	9.3×10^{-11} Wm^{-2} at 1 m	Nicol, 1958c

TABLE 1 — Continued

Group	Species	Peak wavelength, nm	Intensity	Reference
(Hydrozoa—Cont.)	Aequoria forskalea	508	—	Morin & Hastings, 1971
Siphonophora	Vogtia glabra	470	1.2×10^{-9} Wm^{-2} at 1 m	Nicol, 1958c
	V. spinosa	470	3.2×10^{-9} Wm^{-2} at 1 m	Nicol, 1958c
	Rosacea plicata	—	13.7×10^{-11} Wm^{-2} at 1 m	Nicol, 1958c
	Hippopodius hippopus	—	4.2×10^{-11} Wm^{-2} at 1 m	Nicol, 1958c
Scyphozoa	Atolla wyvillei	470	2×10^{-9} Wm^{-2} at 1 m	Nicol, 1958c
	Periphylla periphylla	—	0.68×10^{-9} Wm^{-2} at 1 m	Clarke, et al., 1962
Anthozoa	Pennatula phosphorea	510	62.8×10^{-15} Jm^{-2}	Nicol, 1958b
	Virgularia mirabilis	—	12×10^{-10} Wm^{-2} at 1 m	Nicol, 1958b
	Renilla reniformis	509	—	Cormier, Hori & Anderson, 1974
Ctenophora	Beroë ovata	510	85×10^{-9} Wm^{-2} at 1 m	Nicol, 1958c
	Mnemiopsis leidyi	490	1.9×10^{-7} Wm^{-2} at 1 m	Nicol, 1962
Polychaeta	Harmothoë langirelis	515	—	Nicol, 1957a
	Polynoë scolopendrina	515	—	Nicol, 1957a
	Acholoë astericola	—	1.11×10^{-10} Jm^{-2}	Nicol, 1958a
	Lagisca extenuata	—	1.8×10^{-12} Jm^{-2}	Nicol, 1958a
	Odontosyllis enopla	507	—	Cormier & Totter, 1964
	Chaetopteris variopedatus	465	—	Nicol, 1957b
Lamellibranchiata	Pholas dactylus	480	—	Cormier & Totter, 1964
Cephalopoda	—	from blue to red, depending on species	—	Harvey, 1952
Crustacea (Ostracoda)	Cypridina hilgendorfii	462	—	Shimomura, Johnson & Masugi, 1969
Crustacea (Copepoda)	Metridia lucens	—	5.9×10^{-9} Wm^{-2} at 1 m	Clarke, et al., 1962

TABLE 1 — Continued

Group	Species	Peak wavelength, nm	Intensity	Reference
Crustacea (Copepoda)—(Cont.)	M. longa	—	9.8×10^{-9} Wm^{-2} at 1 m	Clarke, et al., 1962
	M. princeps	—	21.4×10^{-9} Wm^{-2} at 1 m	Clarke, et al., 1962
	Pleuromamma robusta	—	0.11×10^{-9} Wm^{-2} at 1 m	Clarke, et al., 1962
	P. xiphias	—	2.9×10^{-9} Wm^{-2} at 1 m	Clarke, et al., 1962
	Lucicutia grandis	—	1.6×10^{-9} Wm^{-2} at 1 m	Clarke, et al., 1962
	Euaugaptilus magnus	—	1.5×10^{-9} Wm^{-2} at 1 m	Clarke, et al., 1962
	Heterorhabdus spp.	—	0.27×10^{-9} Wm^{-2} at 1 m	Clarke, et al., 1962
	Heterostylites longicornis	—	0.27×10^{-9} Wm^{-2} at 1 m	Clarke, et al., 1962
Crustacea (Decapoda)	Acanthephyra purpuria	—	8.2×10^{-11} Wm^{-2} at 1 m	Nicol, 1958c
	A. pelagica	—	25×10^{-9} Wm^{-2} at 1 m	Clarke, et al., 1962
Crustacea (Euphausiacea)	Euphausia pacifica	476	2.0×10^{-9} Wm^{-2} at 1 m	Kampa & Boden, 1957
	Thysanoëssa raschii	476	—	Boden & Kampa, 1959
	Meganyctiphanes norvegica	476	0.3×10^{-9} Wm^{-2} at 1 m	Clarke, et al., 1962
Urochordata	Pyrosoma atlanticum	482	40×10^{-9} Wm^{-2} at 1 m	Kampa & Boden, 1957
Teleostii	Searsia schnakenbecki	—	4.3×10^{-9} Wm^{-2} at 1 m	Nicol, 1958c
	S. koefoedi	—	28×10^{-9} Wm^{-2} at 1 m	Nicol, 1958c
	Myctophum punctatum	470	52×10^{-11} Wm^{-2} at 1 m	Nicol, 1958c
	Apogon ellioti	460	—	Sie, et al., 1961
	Porichthys spp.	—	1.4×10^{-9} W	Baguet & Case, 1971

Systematic studies have been undertaken in two regions—the Indian Ocean, as part of the International Indian Ocean Expedition, and the Barents Sea. Unfortunately, the scientists involved in these studies were not concerned with bioluminescence as such, but were simply looking at the distribution of various planktonic organisms. Nevertheless, the maps covering these regions (Figs. 5, 12, and 14) show that bioluminescent organisms occurred throughout both areas and in the Indian Ocean throughout the year as well. If such systematic studies were performed in other oceans, it is likely that similar results could be expected.

CONCLUSIONS

The reported observations of bioluminescence and bioluminescent organisms have been largely the result of chance. The location of sampling sites has been largely a matter of opportunity. But even from these facts, it can be seen that luminescence is extremely widespread. Dinoflagellates and euphausiids appear to be the most widely distributed causative organisms. The current development of LLLII's permits luminescence to be detected even when it is not visible to the naked eye. This new tool has the potential for greatly increasing the information to be derived from temporal and areal studies, and, when airborne, provides an opportunity for rapid synoptic observations.

ACKNOWLEDGMENTS

I wish to thank Robert Staples of the Naval Oceanographic Office, Catherine Gordon of the Naval Oceanographic Research and Development Agency, Dr. Frank Wittmann of the National Marine Fisheries Service, and Lt. James Carlson of the Naval Postgraduate School in Monterey, California, all of whom were especially diligent in relating to me not only their sightings but also the observations made by others, of which I might not otherwise have been informed.

BIBLIOGRAPHY

Artemkin, A. S., E. P. Baldina, V. N. Greze and V. S. Filimonov. 1965. Preliminary Results of Investigations of Luminescence in Plankton of Davis Strait and the Caribbean Sea. *Akad. Nauk. Ukrain. SSR, Morskoy Gidrofiz. Inst., Issle. v. Atlantich. Okeane, Ekspress-Inform.* 1:81-91. 1971. Trans. in *Mar. Res. in the Caribbean*, pp. 30-39.

Baguet, Fernand, and James Case. 1971. Luminescence Control in Porichthys (Teleostei): Excitation of Isolated Photophores. *Biol. Bull.* 140:15-27.

Barnes, Anthony T., and James F. Case. 1972. Bioluminescence in the Mesopelagic Copepod, *Gaussia princeps* (T. Scott). *J. Exp. Mar. Biol. Ecol.* 8:53-71.

Bityukov, E. P. 1971. Bioluminescence in a Ship Wake in the Atlantic Ocean and in the Mediterranean and Black Seas. *Oceanology* 11:103-108.

Bityukov, E. P., V. P. Rybasov and V. G. Shaida. 1967. Annual Variations of the Bioluminescence Field Intensity in the Neritic Zone of the Black Sea. *Oceanology* 7:848-856.

Boden, Brian P. 1969. Observations of Bioluminescence on Sond 1965 Cruise of R.R.S. "Discovery." *J. Mar. Biol. Asso. UK* 49:669-682.

Boden, Brian P. 1970. Bioluminescence in Sonic-Scattering Layers. *Proc. Int. Symp. Biol. Sound Scattering*, pp. 60-68.

Boden, Brian P., and Elizabeth M. Kampa. 1959. Spectral Composition of the Luminescence of the Euphausiid Thysanoessa raschii. *Nature* 184:1321-1322.

Bowman, Thomas E. 1967. Bioluminescence in Two Species of Pelagic Amphipods. *J. Fish. Res. Bd. Canada* 24:687-688.

Brinton, E., and K. Gopalakrishnan. 1973. The Distribution of Indian Ocean Euphausiids. *The Biology of the Indian Ocean*. Bernt Zeitschel, editor. Springer-Verlag, New York. pp. 357-382.

Bruce, James A. 1969. Plankton Distribution in the Barents Sea July-August 1963. *Naval Oceanographic Office* Informal Report, IR No. 69-45.

Bruce, James A. 1970a. Bioluminescent Plankton in a Sample Collected East of Barbuda, Leeward Islands, Lesser Antilles. *Naval Oceanographic Office* Biology Laboratory Item B-13.

Bruce, James A. 1970b. Plankton Distribution in the Mediterranean Sea 1962-1963. *Naval Oceanographic Office* Informal Report IR No. 70-30.

Clarke, George L., R. J. Conover, C. N. David and J. A. C. Nicol. 1962. Comparative Studies of Luminescence in Copepods and Other Pelagic Marine Animals. *J. Mar. Biol. Assoc. UK* 42:541-564.

Compton, Andrew Jerome. 1974. A Study of the Bioluminescence of a Deep Scattering Layer Organism (Euphausia pacifica) in Monterey Bay, CA. M. S. Thesis, Naval Postgraduate School, Monterey, CA.

Cormier, Milton J., and John R. Totter. 1964. Bioluminescence. *Ann. Rev. Biochem.* 33:431-458.

Cormier, Milton J., Kazuo Hori and James M. Anderson. 1974. Bioluminescence in Coelenterates. *Biochem. Biophys. Acta* 346:137-164.

Cram, D. L. 1972. The Role of Aircraft-Borne Remote Sensors in South African Fisheries Research. Proc. Symp. S62 Remote Sensing, Pretoria CSIR, pp. 129-134.

Cram, David. 1973. Pilchard Stocks Surveyed by Remote Sensors. *Fishing News International* 12(3):73-75.

Cram, D. L. 1974. Rapid Stock Assessment of Pilchard Populations by Aircraft-Borne Remote Sensors. Proc. 9th Internat'l Symp. on Remote Sensing of Environment, pp. 1043-1050.

Cram, D. L., and J. Hampton. 1976. A Proposed Aerial/Acoustic Strategy for Pelagic Fish Stock Assessment. *J. Cons. Int. Explor. Mer.* 37(1):91-97.

DeDecker, A. 1973. Agulhas Bank Plankton. *The Biology of the Indian Ocean*. Bernt Zeitschel, Editor. Springer-Verlag, New York. pp. 189-220.

Doyle, Jean D., and R. H. Kay. 1967. Some Studies on the Bioluminescence of the Euphausiids *Meganyctiphanes norvegica* and *Thysanoessa raschii. J. Mar. Biol. Assoc. UK*

Drennan, Kirby L. 17-19 Mar. 1969. Fishery Oceanography from Space. Proc. 6th Space Cong., Cocoa Beach, Florida.

Drennan, Kirby L. 1971. Some Potential Applications of Remote Sensing in Fisheries. *Proc. Symp. Remote Sensing in Mar. Biol. and Fish. Resources*, pp. 25-65.

Eberhard, Anatol. 1972. Inhibition and Activation of Bacterial Luciferase Synthesis. *J. Bacteriol.* **109**:1101-1105.

Eckert, Roger. 1966. Excitation and Luminescence in *Noctiluca miliaris*. *Bioluminescence in Progress*. Frank H. Johnson and Yata Haneda, Editors. Princeton Univ. Press, Princeton, N.J. pp. 269-300.

Eppley, R. W., and W. G. Harrison. 1975. Physiological Ecology of *Gonyaulax polyedra*, a Red Water Dinoflagellate of Southern California. *Proc. First International Conference on Toxic Dinoflagellate Blooms*. Vincent R. LoCicero, Editor. Mass. Science and Technology Foundation, Wakefield, Mass. pp. 11-22.

Erdman, Donald S. 1968. Observations—Blue Lights at Sea. *Bull. Amer. Littoral Soc.* 5:43.

Fowler, S. W., B. Oregioni and J. LaRosa. 1976. Trace Metals in Pelagic Organisms from the Mediterranean Sea. Activities of the International Laboratory of Marine Radioactivity, 1976 Report IAEA-187. pp 110-122.

Foxton, P. 1970. The Vertical Distribution of Pelagic Decapods (Crustacea: Natantia) Collected on the Sond Cruise, 1965. II. The Penaeidea and General Discussion. *J. Mar. Biol. Assoc. UK* **50**:961-1000.

Foxton, P. 1972. Further Evidence of the Taxonomic Importance of the Organs of Pesta in the Genus Sergestes (Natantia, Penaeidea). *Crustaceana* **22**:181-189.

Freeman, Gary, and George T. Reynolds. 1973. The Development of Bioluminescence in the Ctenophore Mnemiopsis leidyi. *Develop. Biol.* **31**:61-100.

Gitel'zon, I. I., O. G. Baklanov, V. S. Filimonov, A. S. Artemkin and V. F. Schatokhin. 1965. Bioluminescence as a Hydrooptical and Biological Factor in the Sea. *Trudy Moskovskogo Obshchestva Ispytoteley Prirody* **21**:147-155.

Gitel'zon, I. I., R. I. Chumakova, V. S. Filimonov, A. S. Artemkin and V. F. Schatokhin. 1967. Instrumental Bioluminescence Measurements in the Tropical Part of the Pacific. Symposium on Bioluminescence in the Pacific Area of the 11th Pacific Science Conference, August 1966. *Sci. Rep. Yokosuka City Mus.* **13**:6-11.

Hamman, J. P., and Howard H. Seliger. 1972. The Mechanical Triggering of Bioluminescence in Marine Dinoflagellates: Chemical Basis. *J. Cell. Physiol.* **80**:397-408.

Haneda, Yata. 1971. The Search for Cypridina on Palau Island. *Sci. Rpt. Yokosuka City Mus.* **16**:29-31.

Haneda, Yata, Frederick I. Tsuji, Noboru Sugiyama and Kazuo Hori. 1973. Observations of Deep Sea Luminous Organisms Collected on the R/V Tansei Maru, Oceanographic Institute of Tokyo Univ. *Sci. Rpt. Yokosuka City Mus.* **20**:4-10.

Haq, S. M., J. Ali Khan and S. Chugtai. 1973. The Distribution and Abundance of Zooplankton along the Coast of Pakistan During Postmonsoon and Premonsoon Periods. *The Biology of the Indian Ocean*. Bernt Zeitschel, Editor. Springer-Verlag, New York. pp. 257-272.

Harvey, E. Newton. 1952. *Bioluminescence.* Academic Press, N.Y.

Herring, P. J. 1967. Luminescence in Marine Amphipods. *Nature* 214:1260-1261.

Herring, Peter J. 1974. New Observations on the Bioluminescence of Echinoderms. *J. Zool. London* 172:401-418.

Herring, Peter J. 1976a. Bioluminescence in Decapod Crustacea. *J. Mar. Biol. Asso. UK* 56:1029-1047.

Herring, Peter J. 1976b. Observations of Bioluminescence at Sea. *Mar. Obs.* 46:176-183.

Ivanov, B. G. 1969. Luminescence of Antarctic Krill (*Euphausia superba*). *Oceanology* 9:413-414.

Johnson, Frank H. 1970. The Bioluminescent Protein "Aequorin." *Naval Res. Rev.* 23:16-23.

Kalle, Kurt. 1960. Die rätselhafte und ,,unheimliche´´Naturerscheinung des explodierenden´´ und des ,,rotierenden´´Meeresleuchtens-eine Folge lokaler Seebeben. *Deutsche Hydrog. Zeits.* 13:49-77.

Kampa, Elizabeth M., and Brian P. Boden. 1957. Light Generation in a Sonic Scattering Layer. *Deep-Sea Res.* 4:78-92.

Karabashev, G. S. 1969. A Photometric Method for Study of Bioluminescence in the Sea. *Oceanology* 9:886-892.

Karabashev, G. S., and A. N. Solv'yev. 1972. Bioluminescence in the Baltic Sea. *Oceanology* 12:776-778.

Kelly, Mahlon G. 1968. The Occurrence of Dinoflagellate Luminescence at Woods Hole. *Biol. Bull.* 135:279-295.

Kelly, Mahlon G., and Steven Katona. 1966. An Endogenous Diurnal Rhythm of Bioluminescence in a Natural Population of Dinoflagellates. *Biol. Bull.* 131:115-126.

Mengers, Paul. 1977. A Digital Boost for LLLTV. *Op. Spectra* 11(8):60-62.

Michel, H. B., and Maria Foyo. 1976. Caribbean Zooplankton. Part I—Siphonophora, Heteropoda, Copepoda, Euphausiacea, Chaetognatha and Salpidae. Office of Naval Research, Washington, D.C.

Mitchell, George W., and J. W. Hastings. 1971. A Stable, Inexpensive, Solid-State Photomultiplier Photometer. *Analyt. Biochem.* 39:243-250.

Morin, James G., and J. Woodland Hastings. 1971. Energy Transfer in a Bioluminescent System. *J. Cell. Physiol.* 77:313-318.

Mulligan, Hugh F. 1975. Oceanographic Factors Associated with New England Red Tide Blooms. *Proc. First International Conference on Toxic Dinoflagellate Blooms.* Vincent R. LoCicero, Editor. Mass. Science and Technology Foundation, Wakefield, Mass. pp. 23-40.

Nair, V. R., and T. S. S. Rao. 1973. Chaetognaths of the Arabian Sea. *The Biology of the Indian Ocean.* Bernt Zeitschel, Editor. Springer-Verlag, New York. pp. 293-317.

Nealson, Kenneth H., Terry Platt and J. Woodland Hastings. 1970. Cellular Control of the Synthesis and Activity of the Bacterial Luminescent System. *J. Bacteriol.* 104:313-322.

Nealson, Kenneth H., Anatol Eberhard and J. W. Hastings. 1972. Catabolite Repression of Bacterial Bioluminescence: Functional Implications. *Proc. Nat. Acad. Sci. U.S.* 69:1073-1076.

Neshyba, Steve. 1967. Comparison of Minimum Detectable Light Levels and the Level of Stimulated Marine Bioluminescence in Ocean Waters. Fourth U.S. Navy Symp. on Military Oceanography, Vol. 1. pp. 428-438.

Nicol, J. A. C. 1957a. Spectral Composition of the Light of Polynoid Worms. *J. Mar. Biol. Assoc. UK.* 36:529-538.

Nicol, J. A. C. 1957b. Spectral Composition of the Light of Chaetopterus. *J. Mar. Biol. Assoc. UK.* 36:629-642.

Nicol, J. A. C. 1958a. Luminescence in Polynoids. IV. Measurements of Light Intensity. *J. Mar. Biol. Assoc. UK.* 37:33-41.

Nicol, J. A. C. 1958b. Observations of the Luminescence of *Pennatula phosphorea*, with a Note on the Luminescence of *Virgularia mirabilis*. *J. Mar. Biol. Assoc. UK.* 37:551-563.

Nicol, J. A. C. 1958c. Observations on Luminescence in Pelagic Animals. *J. Mar. Biol. Assoc. UK.* 37:705-752.

Nicol, J. A. C. 1962. Animal Luminescence. *Adv. in Comp. Physiol. and Biochem.* Vol. 1. O. Lowenstein, Editor, Academic Press. New York and London. pp. 217-273.

Oguri, M., D. Soule, D. M. Juge and B. C. Abbott. 1975. Red Tides in the Los Angeles-Long Beach Harbor. *Proc. First International Conference on Toxic Dinoflagellate Blooms.* Vincent R. LoCicero, Editor. Mass. Science and Technology Foundation, Wakefield, Mass. pp. 41-46.

Petersson, Göran. 1968. Studies on Photophores in the Euphausiacea. *Sarsia* 36:1-39.

Roithmayr, Charles M. 1970. Airborne Low-Light Sensor Detects Luminescing Fish Schools at Night. *Commercial Fisheries Rev.* 32:42-51.

Roithmayr, Charles M. 1971. Low Light Level Image Intensification System for Coastal Fish Stock Assessment. Second Nat. Coastal and Shallow-Water Res. Conf. Abstr. p. 191.

Roithmayr, Charles M., and Frank P. Wittmann. 1972. Low Light Level Sensor Developments for Marine Resource Assessment. Marine Technology Soc. 8th Ann. Conf. Preprints, pp. 277-288.

Rudyakov, Yu. A. 1967. Procedure for Studying the Bioluminescence of the Sea. *Oceanology* 7:569-577.

Rudyakov, Yu A. 1968. Bioluminescence Potential and Its Relation to Concentration of Luminescent Plankton. *Oceanology* 8:710-715.

Rudyakov, Yu A., and N. M. Voronina. 1967. Plankton and Bioluminescence in the Red Sea and the Gulf of Aden. *Oceanology* 7:838-848.

Saraswathy, M. 1973. Distribution of Gaussia (Copepoda, Metridiidae) in the Upper 200 m in the Indian Ocean. *The Biology of the Indian Ocean.* Bernt Zeitschel, Editor. Springer-Verlag, New York. pp. 335-338.

Seliger, Howard H., W. H. Biggley and E. Swift. 1969. Absolute Values of Photon Emission from the Marine Dinoflagellates *Pyrodinium bahamense*, *Gonyaulax polyedra*, and *Pyrocystis lunula*. *Photochem. Photobiol.* 10:227-232.

Seliger, Howard H., W. G. Fastie, W. R. Taylor and William D. McElroy. 1962. Bioluminescence of Marine Dinoflagellates. I. An Underwater Photometer for Day and Night Measurements. *J. Gen. Physiol.* 45:1003-1017.

Shimomura, Osamu, and Frank H. Johnson. 1967. Extraction, Purification, and Properties of the Bioluminescence System of the Euphausiid Shrimp *Meganyctiphanes norvegica*. *Biochemistry* 6:2293-2306.

Shimomura, Osamu, and Frank H. Johnson. 1968. Light-Emitting Molecule in a New Photoprotein Type of Luminescence System from the Euphausiid Shrimp *Meganyctiphanes norvegica*. *Proc. Nat. Acad. Sci. U.S.* 59:475-477.

Shimomura, Osamu, Frank H. Johnson and Takashi Masugi. 1969. Cypridina Bioluminescence: Light-Emitting Oxyluciferin-Luciferase Complex. *Science* 164:1299-1300.

Sie, Edward H.-C., William D. McElroy, Frank H. Johnson and Yata Haneda. 1961. Spectroscopy of the *Apogon* Luminescent System and of Its Cross-Reaction with the *Cypridina* System. *Arch. Biochem. Biophys.* 93:286-291.

Staples, Robert. 1966. The Distribution and Characteristics of Surface Bioluminescence in the Oceans. Naval Oceanographic Office Rpt. TR-184.

Steidinger, Karen A. 1975. Basic Factors Influencing Red Tides. *Proc. First International Conference on Toxic Dinoflagellate Blooms*. Vincent R. LoCicero, Editor. Mass. Science and Technology Foundation, Wakefield, Mass. pp. 153-162.

Stevenson, Merritt R. 1975. A Review of Some Uses of Remote Sensing in Fishery Oceanography and Management. *IEEE Ocean* 75:467-472.

Sweeney, Beatrice M. 1975. Red Tides I Have Known. *Proc. First International Conference on Toxic Dinoflagellate Blooms*. Vincent R. LoCicero, Editor. Mass. Science and Technology Foundation, Wakefield, Mass. pp. 225-234.

Swift, Elijah, William H. Biggley and Howard H. Seliger. 1973. Species of Oceanic Dinoflagellates in the Genera *Dissodinium* and *Pyrocystis:* Interclonal and Interspecific Comparisons of the Color and Photon Yield of Bioluminescence. *J. Phycol.* 9:420-426.

Taylor, F. J. R. 1973. General Features of Dinoflagellate Material Collected by the "Anton Bruun" during the International Indian Ocean Expedition. *The Biology of the Indian Ocean*. Bernt Zeitschel, Editor. Springer-Verlag, New York. pp. 155-170.

Tett, Paul. 1969a. Dinoflagellate Bioluminescence. Ph.D. Thesis. Univ. of Glasgow. 360 pages.

Tett, P. B. 1969b. The Effects of Temperature upon the Flash-Stimulated Luminescence of the Euphausiid *Thysanoessa raschi*. *J. Mar. Biol. Assoc. UK.* 49:245-258.

Tett, P. B. 1971. The Relation Between Dinoflagellates and the Bioluminescence of Sea Water. *J. Mar. Biol. Assoc. UK.* 51:183-206.

Tett, P. B. 1972. An Annual Cycle of Flash-Induced Luminescence in the Euphausiid *Thysanoessa raschi*. *Mar. Biol.* 12:207-218.

Tett, P. B., and Mahlon G. Kelly. 1973. Marine Bioluminescence. *Oceanog. Mar. Biol. Ann. Rev.* 11:89-173.

Tibbs, John F. 1967. On Some Planktonic Protozoa Taken from the Track of Drift Station ARLIS-I, 1960-61. *Arctic* 20:247-254.

Tsuji, Frederick I., Richard V. Lynch and Yata Haneda. 1970. Studies on the Bioluminescence of the Marine Ostracod Crustacean *Cypridina serrata*. *Biol. Bull.* 139:386-401.

Tsuji, Frederick I., Yata Haneda, Richard V. Lynch and Noboru Sugiyama. 1971. Luminescence Cross-Reactions of *Porichthys* Luciferin and Theories on the Origin of Luciferin in Some Shallow-Water Fishes. *Comp. Biochem. Physiol.* 40A:163-179.

Turner, R. J. 1965. Notes on the Nature and Occurrence of Marine Bioluminescent Phenomena. NIO Internal Report #B4. National Institute of Oceanography, Wormley, Godalming, Surrey.

Turner, R. J. 1966. Marine Bioluminescence. *Mar. Obs.* 36:20-29.

Verploegh, George. 1968. The Phosphorescent Wheel. *Deutsche Hydrog. Zeits.* 21(Heft4):153-162.

Vinogradov, M. E., I. I. Gitel'zon, and Yu I. Sorokin. 1970. The Vertical Structure of a Pelagic Community in the Tropical Ocean. *Marine Biology* 6:187-194.

Voytov, V. I. 1967. Some Results of an Expedition on the R/V *Akademik S. Vavilov* in the Red Sea and the Mediterranean. *Oceanology* 7:271-276.

Wardle, William J., Sammy M. Ray and Anita S. Aldrich. 1975. Mortality of Marine Organisms Associated with Offshore Summer Blooms of the Toxic Dinoflagellate *Gonyaulax monilata* Howell at Galveston, Texas. *Proc. First International Conference on Toxic Dinoflagellate Blooms*. Vincent R. LoCicero, Editor. Mass. Science and Technology Foundation, Wakefield, Mass. pp. 257-263.

Yentsch, Charles S., and J. C. Laird. 1968. Seasonal Sequence of Bioluminescence and the Occurrence of Endogenous Rhythms in Oceanic Waters off Woods Hole, Mass. *J. Mar. Res.* 26:127-133.

Youngbluth, Marsh J. 1976. Vertical Distribution and Diel Migration of Euphausiids in the Central Region of the California Current. *Fish Bull.* 74:925-936.

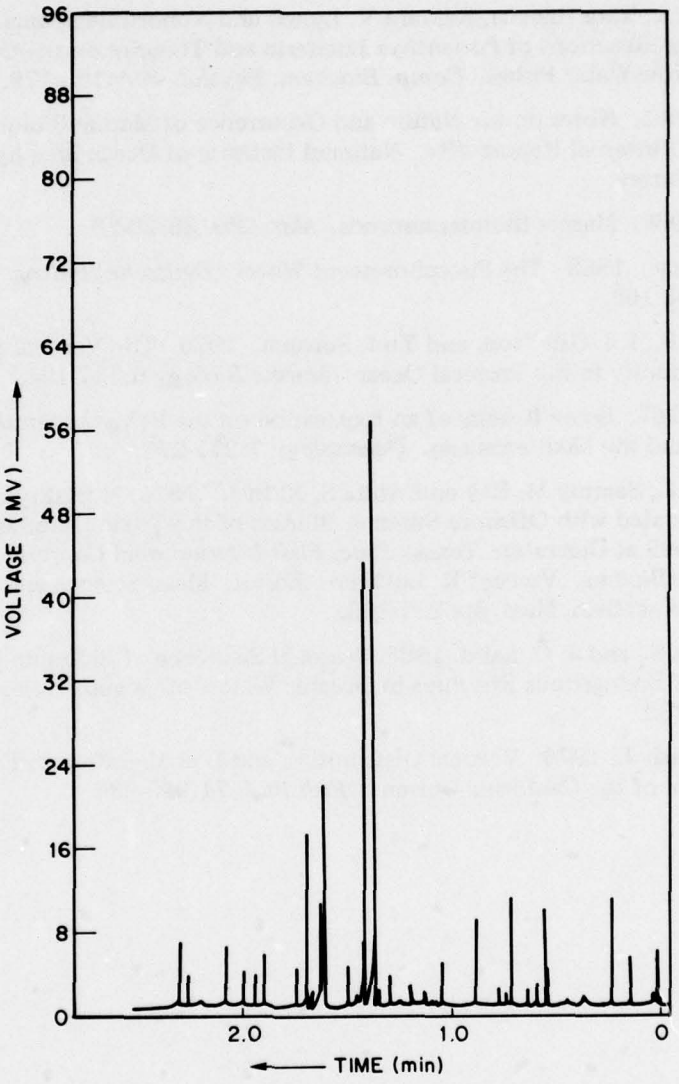


Fig. 1 — Typical pattern of spontaneous flashing of a sample of luminous organisms from a plankton tow

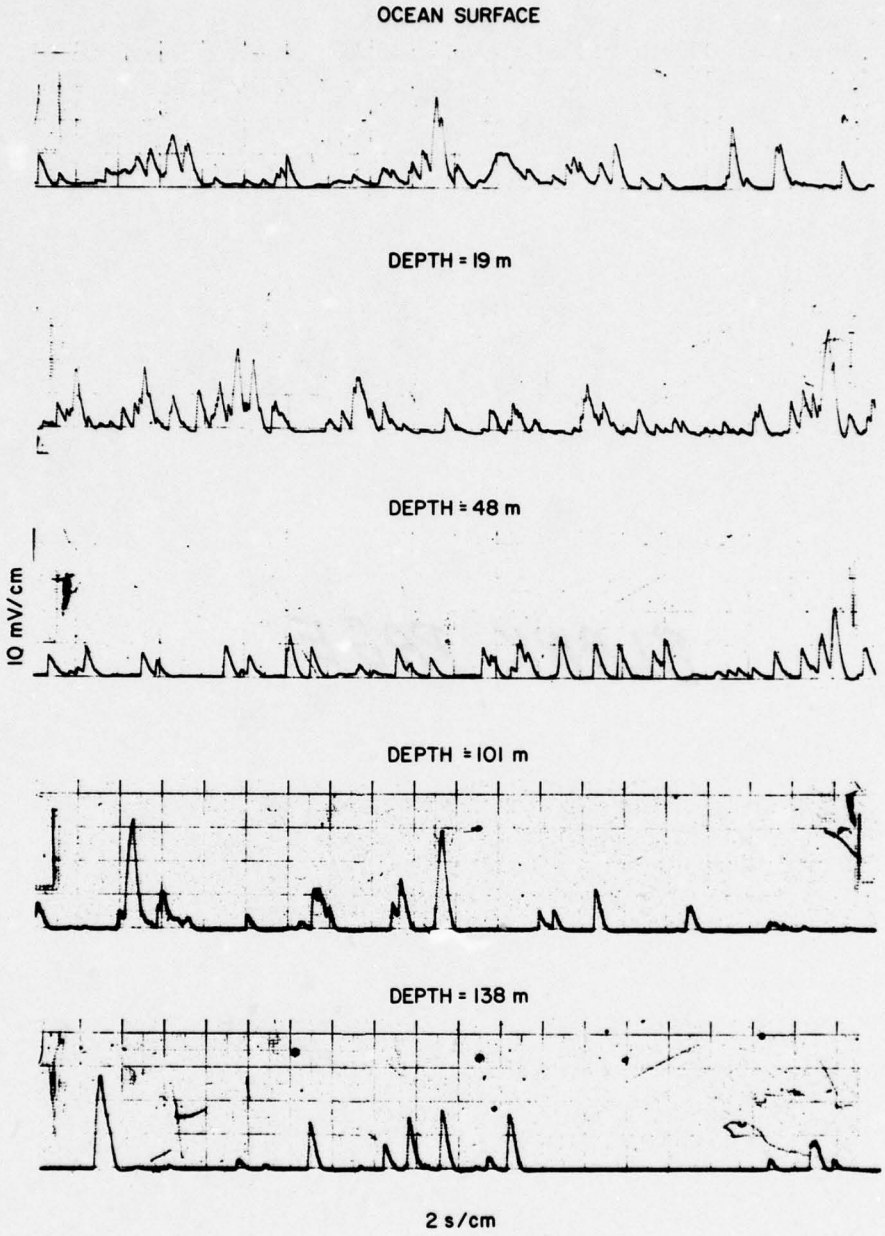


Fig. 2 — A typical pattern of stimulated flashing at various ocean depths

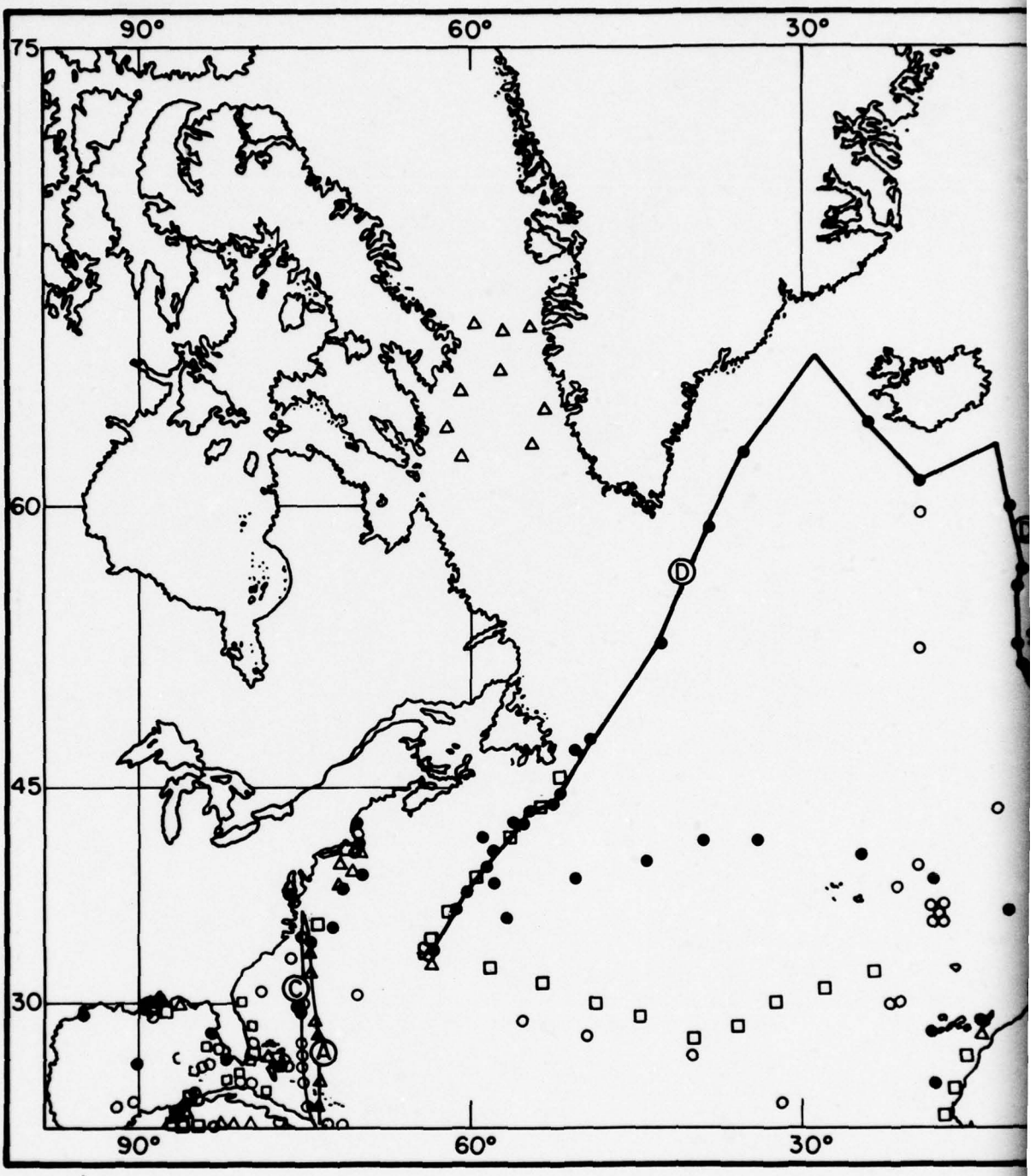
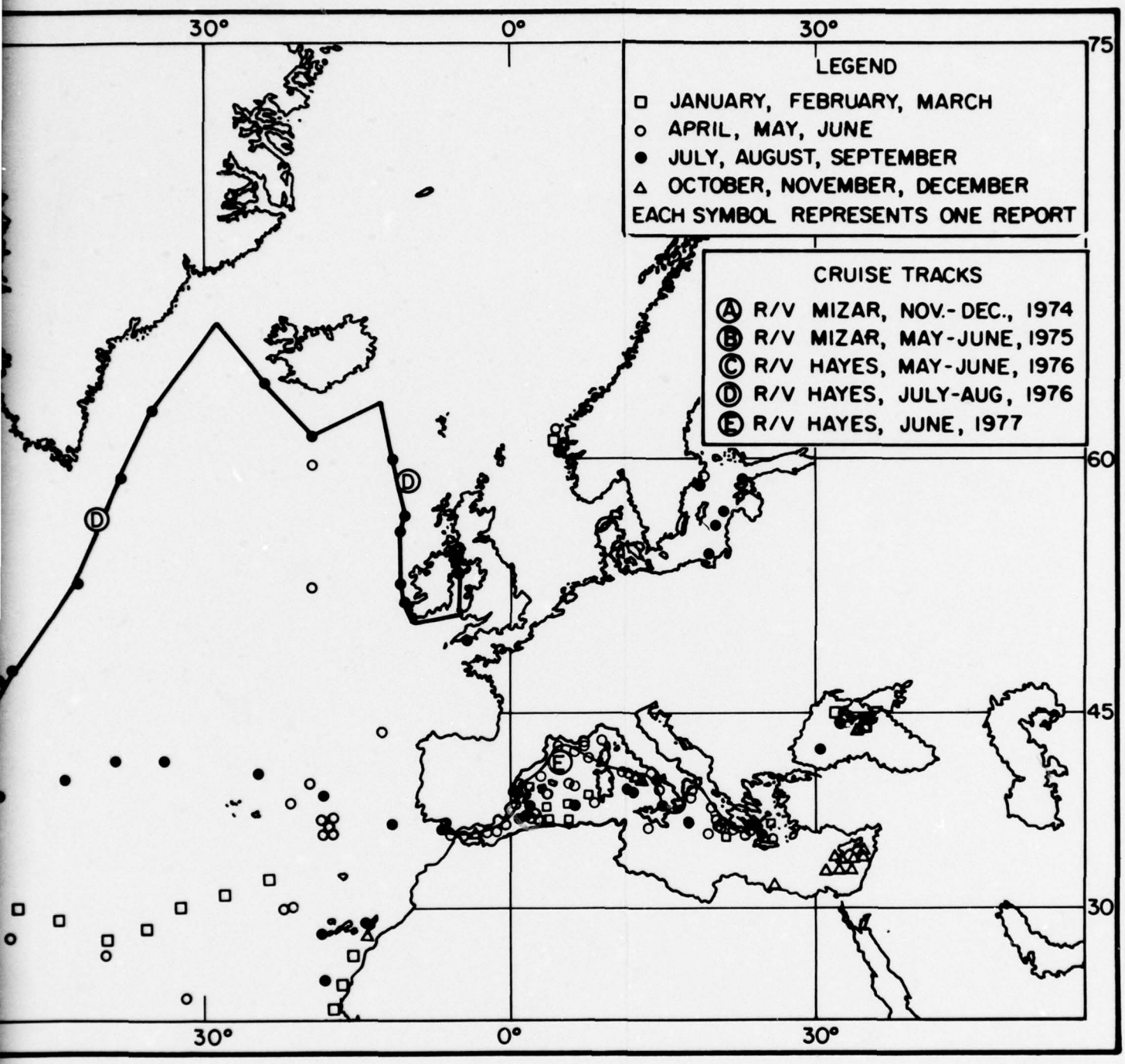


Fig. 3 — Seasonal distribution of bioluminescence in the northern



asonal distribution of bioluminescence in the northern Atlantic Ocean and adjacent seas

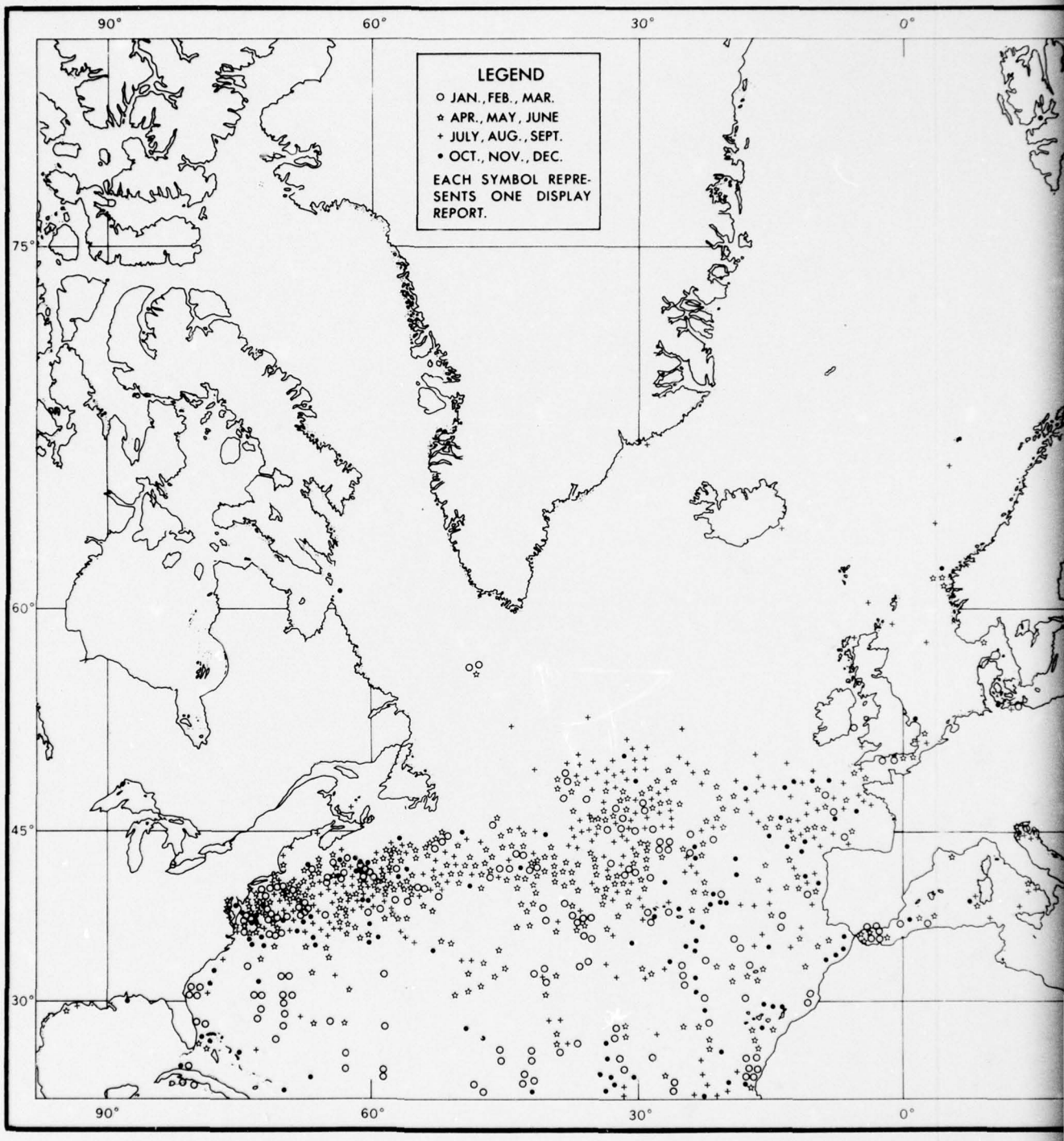
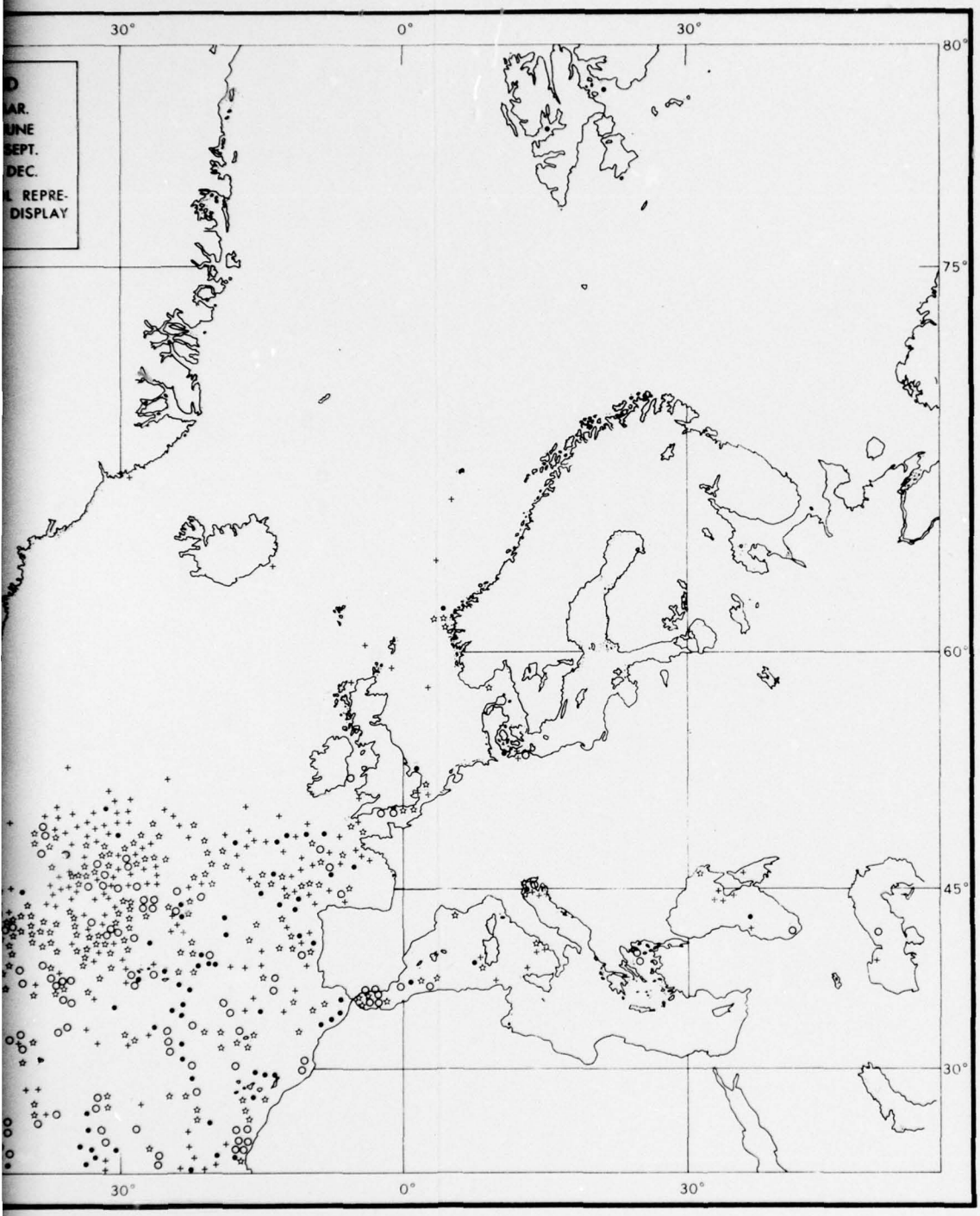


Fig. 4 — Seasonal distribution of bioluminescent displays in the northern Atlantic Ocean and adjacent sea



minescent displays in the northern Atlantic Ocean and adjacent seas (Staples, 1966)

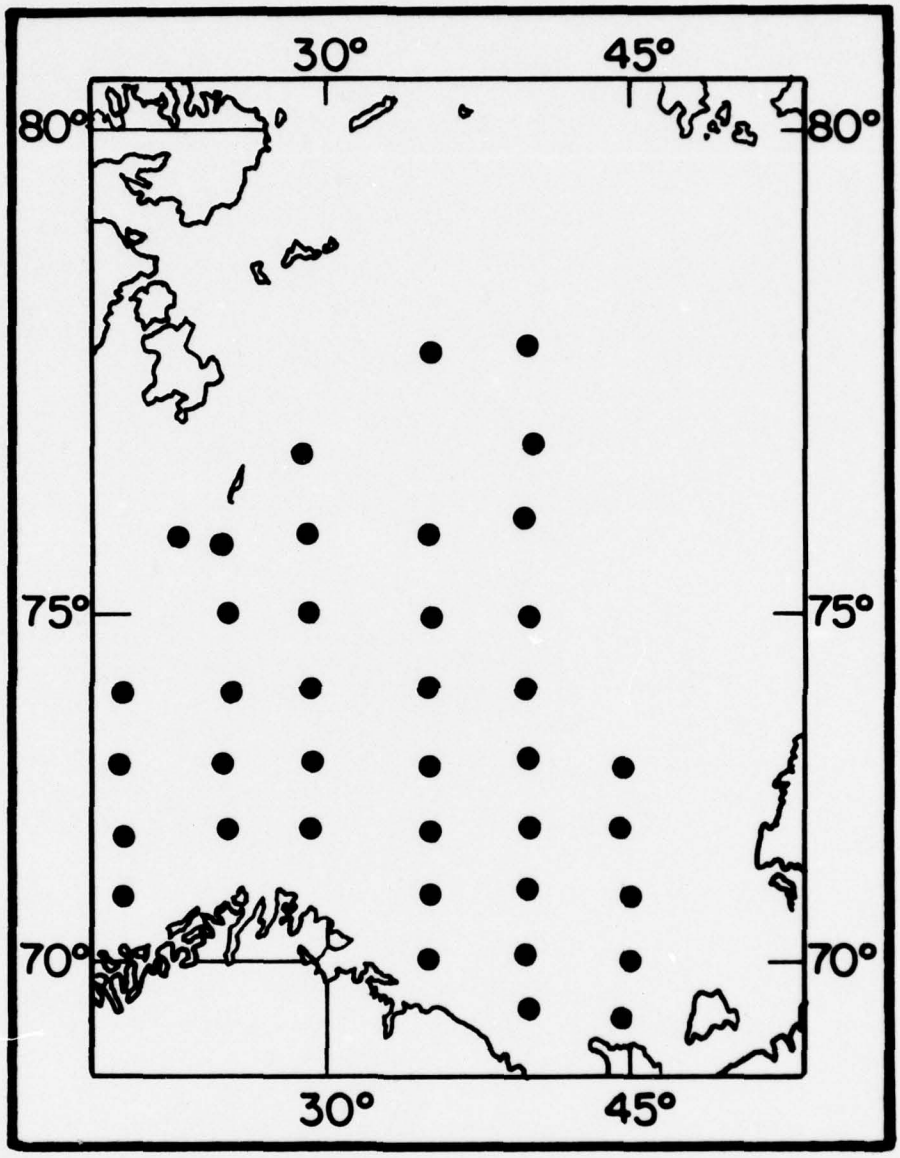


Fig. 5—Distribution of bioluminescence in the Barents Sea

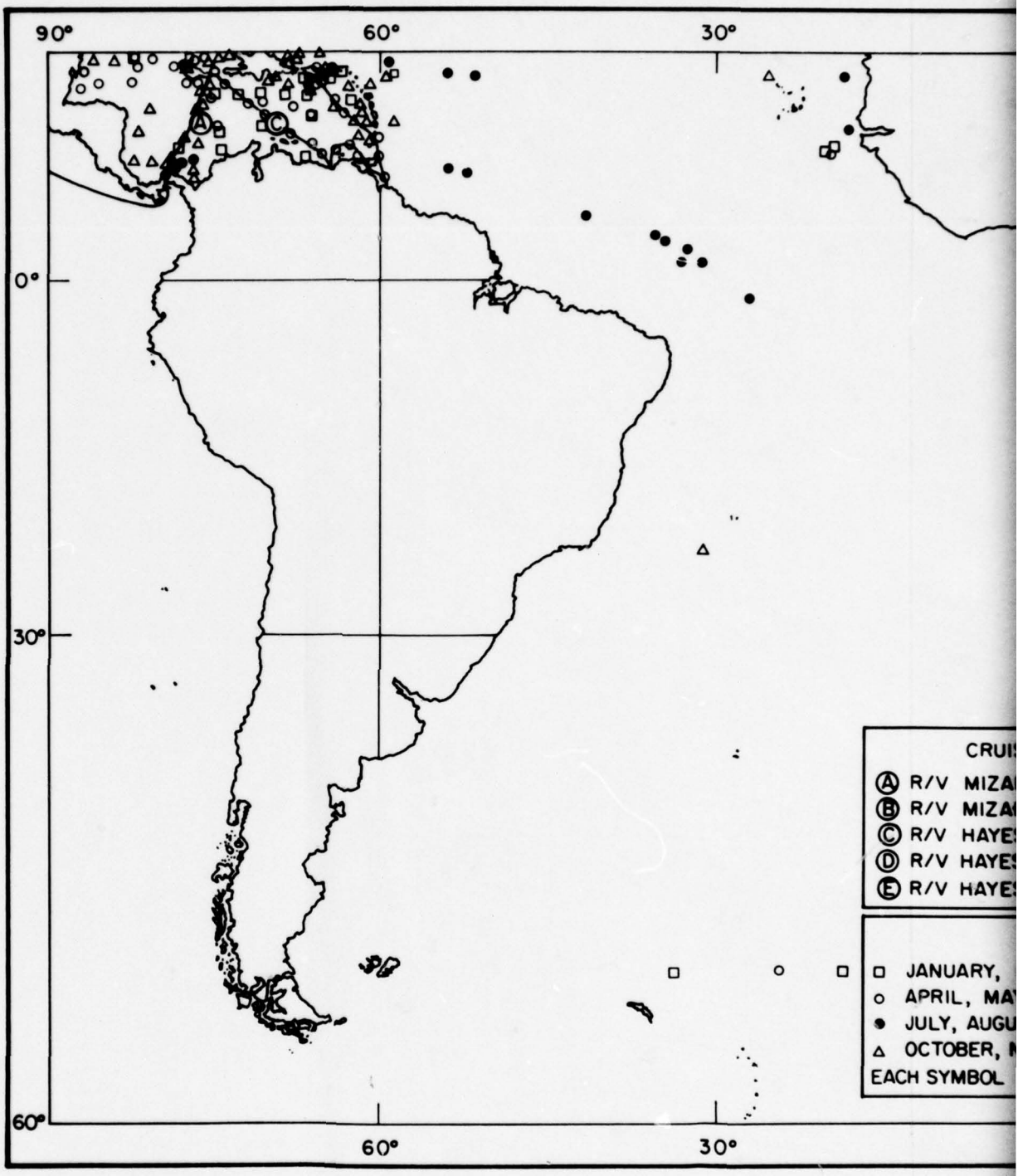
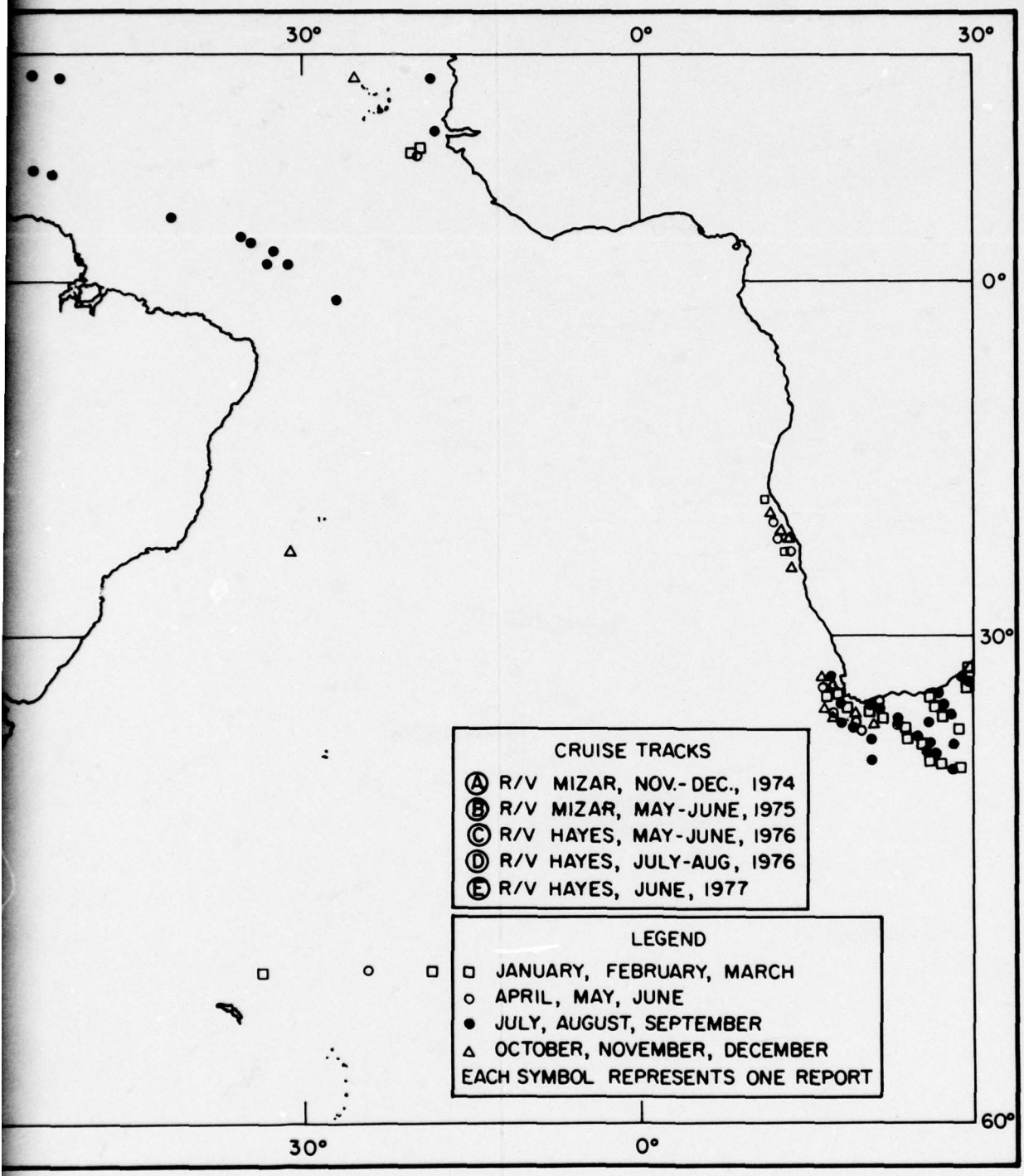


Fig. 6 — Seasonal distribution of bioluminescence in the southern north Atlantic and sou

(Page 28 Blank)



al distribution of bioluminescence in the southern north Atlantic and south Atlantic Oceans

(Page 28 Blank)

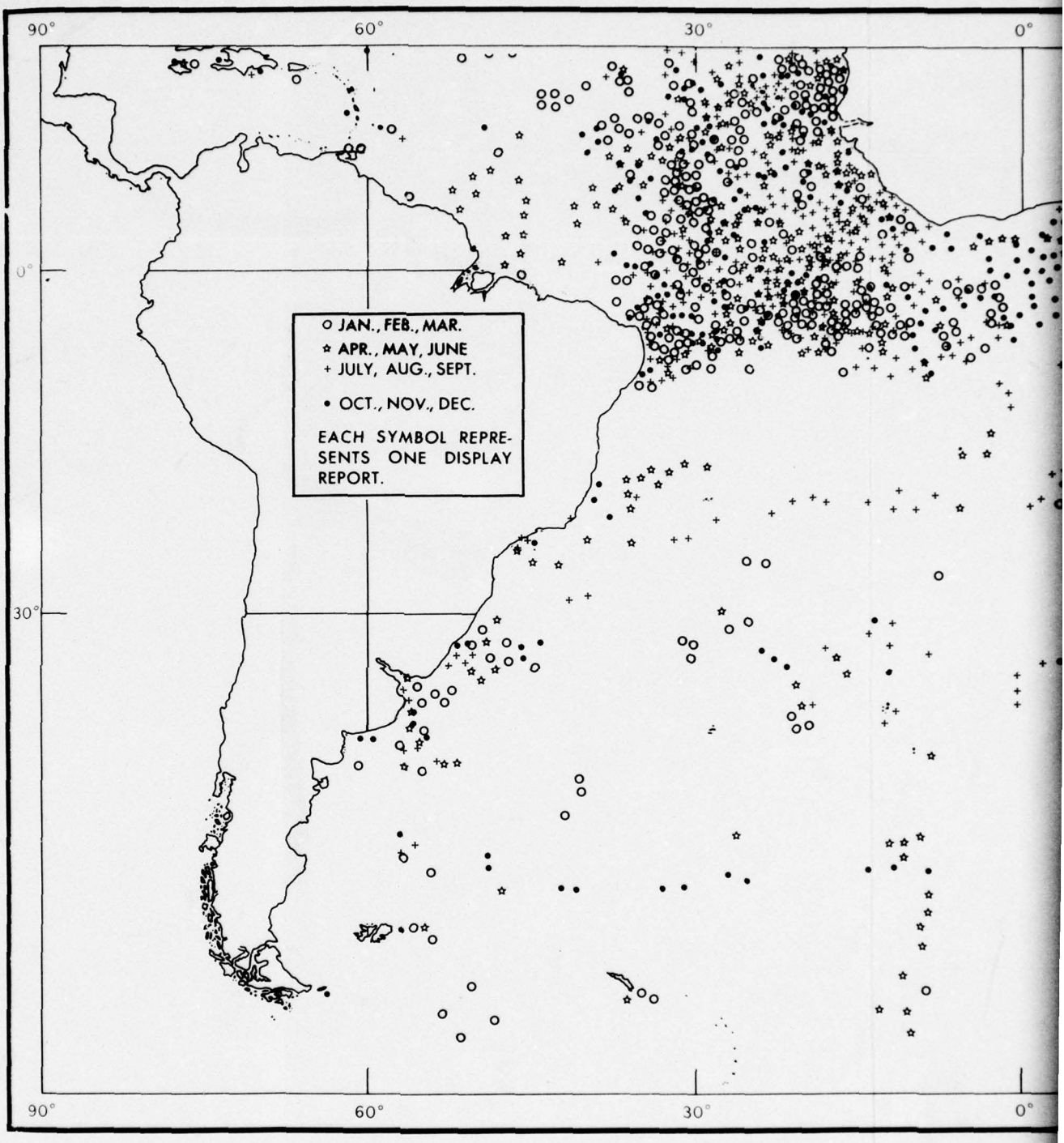
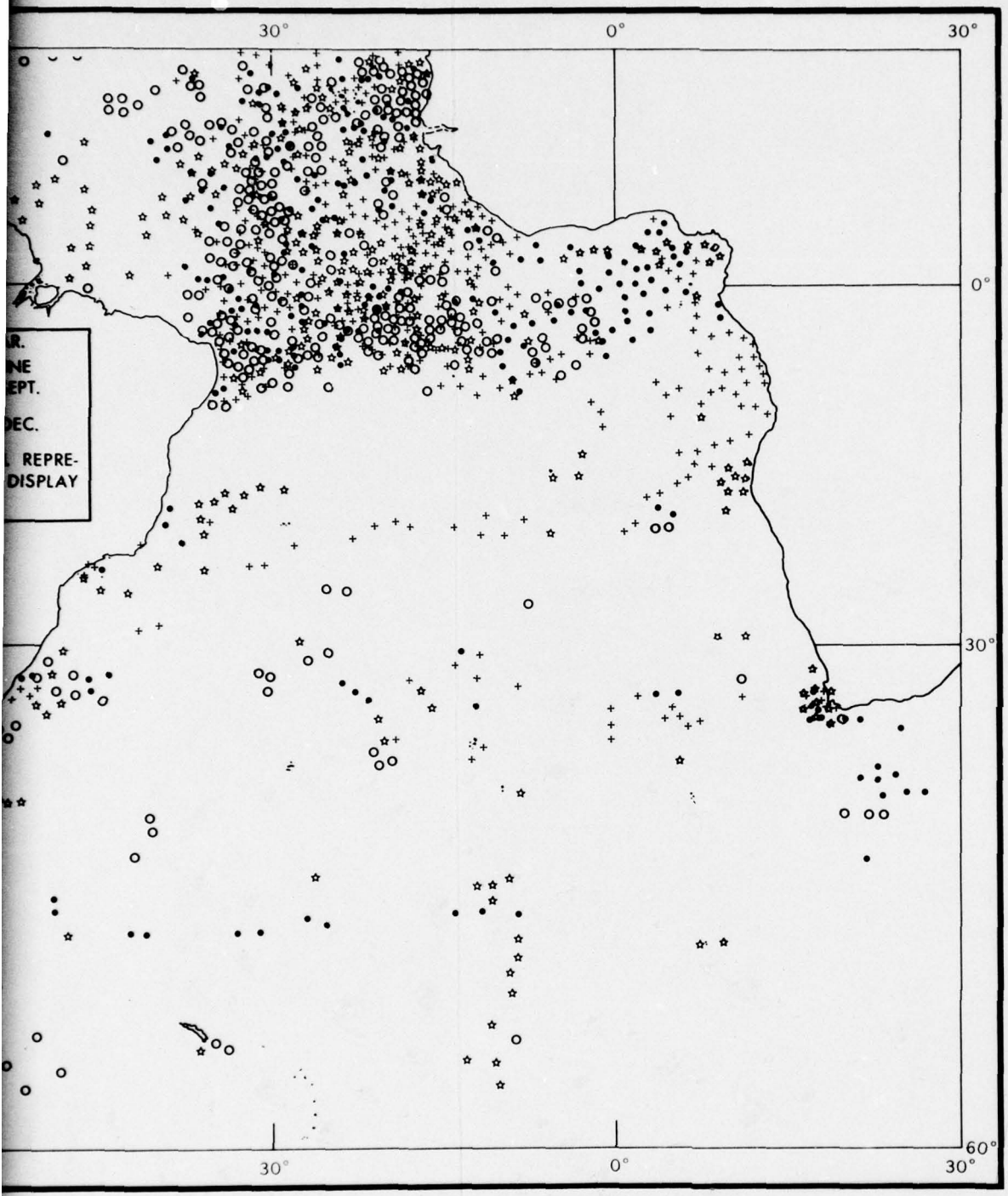


Fig. 7 — Seasonal distribution of bioluminescent displays in the southern north Atlantic and so
Atlantic Oceans (Staples, 1966)

(Page 30 Blank)



distribution of bioluminescent displays in the southern north Atlantic and south Atlantic Oceans (Staples, 1966)

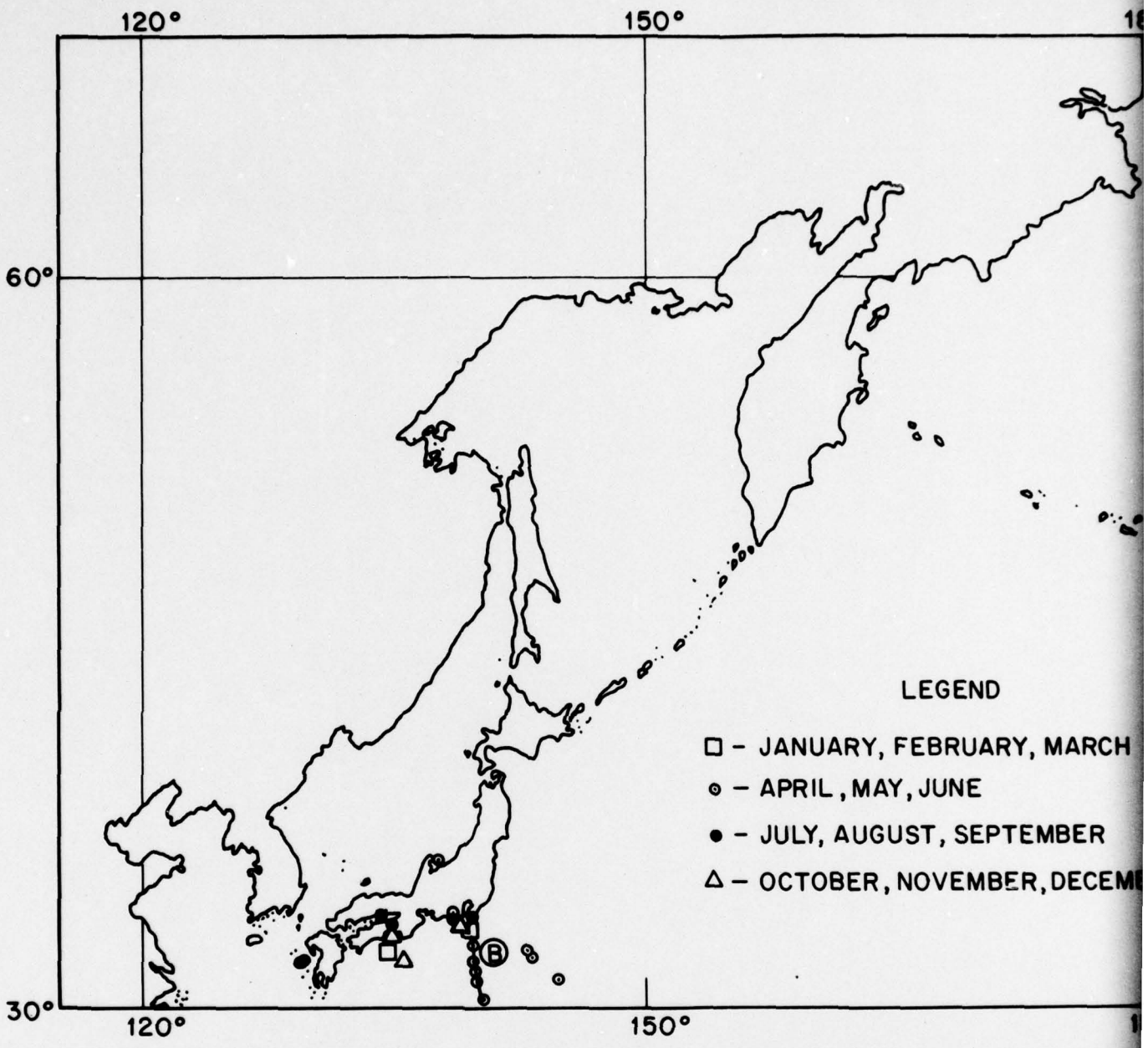
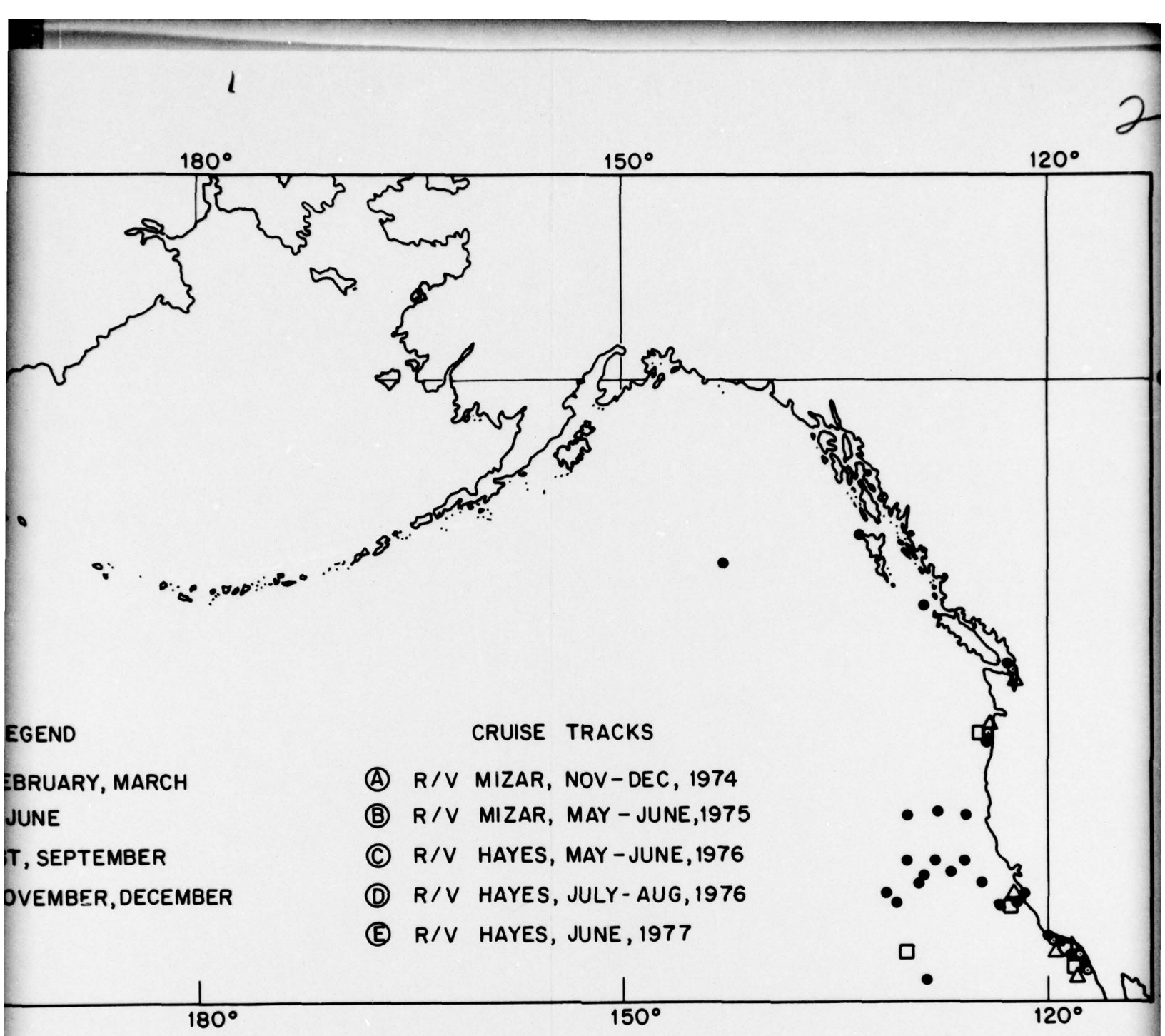
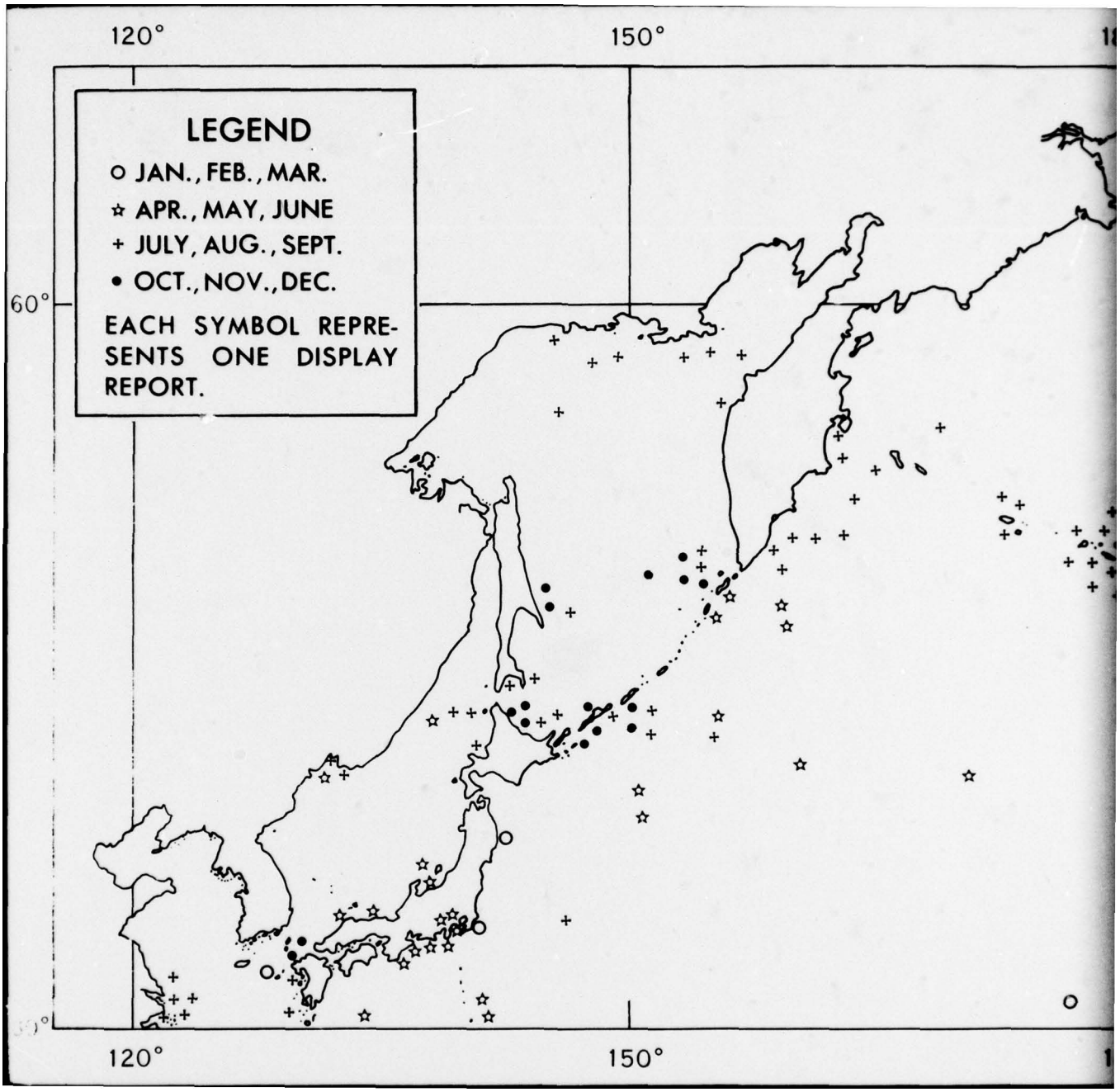


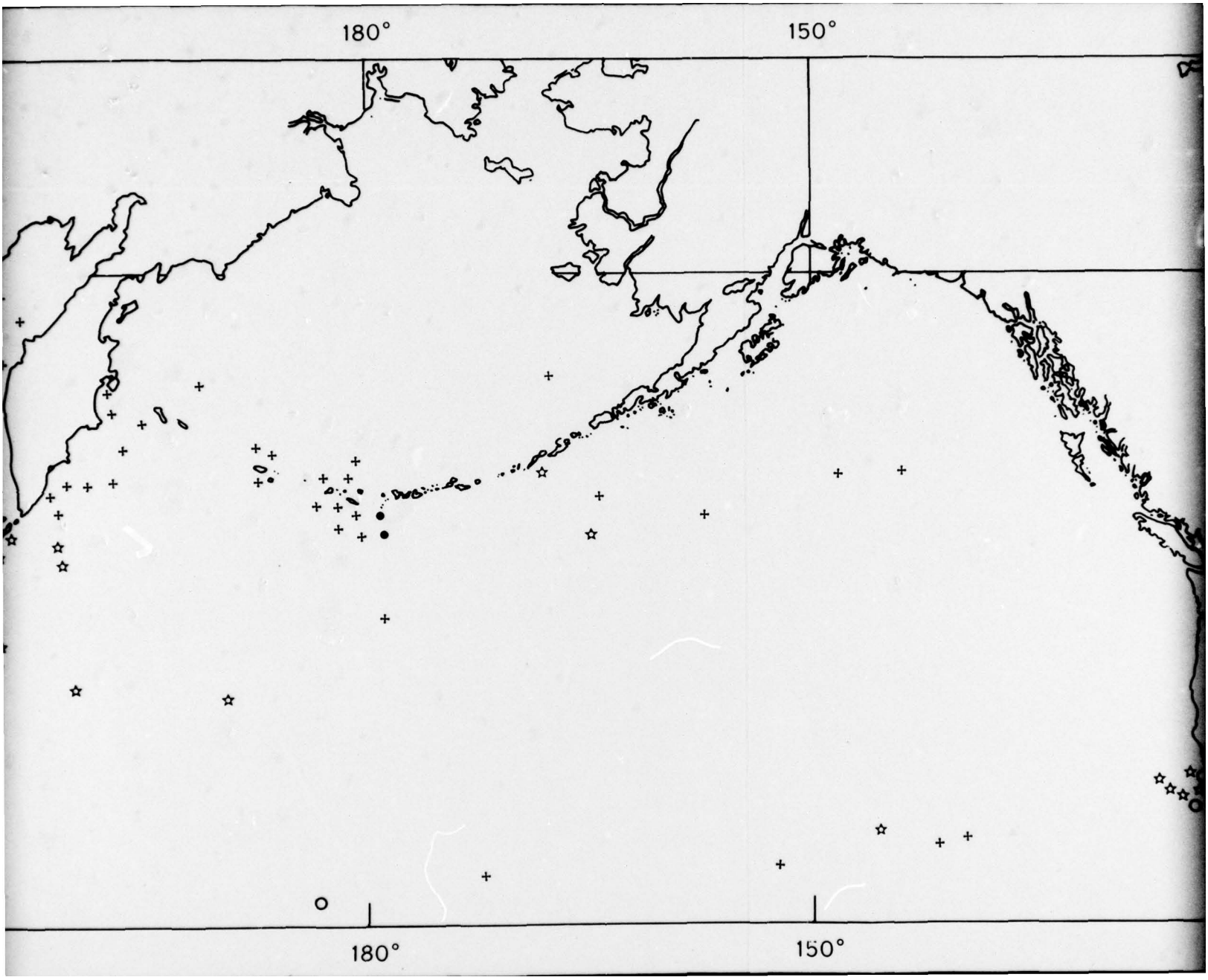
Fig. 8 — Seasonal distribution of biolumines

(Page

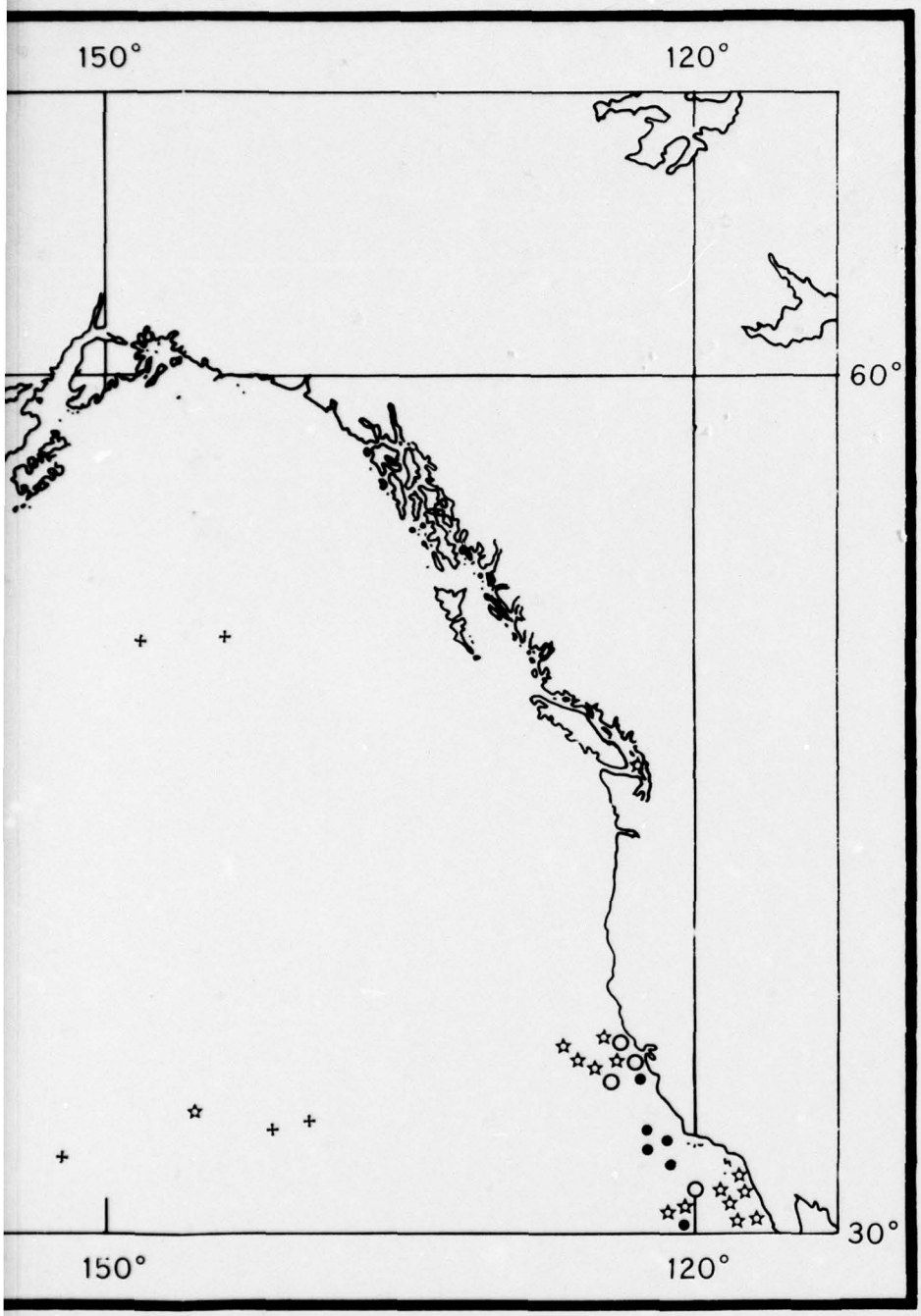


distribution of bioluminescence in the north Pacific Ocean and adjacent seas


120°
150°
60°
LEGEND
o JAN., FEB., MAR.
☆ APR., MAY, JUNE
+ JULY, AUG., SEPT.
• OCT., NOV., DEC.
EACH SYMBOL REPRESENTS ONE DISPLAY REPORT.
120°
150°


180°
150°
180°
150°

3



ples, 1966)

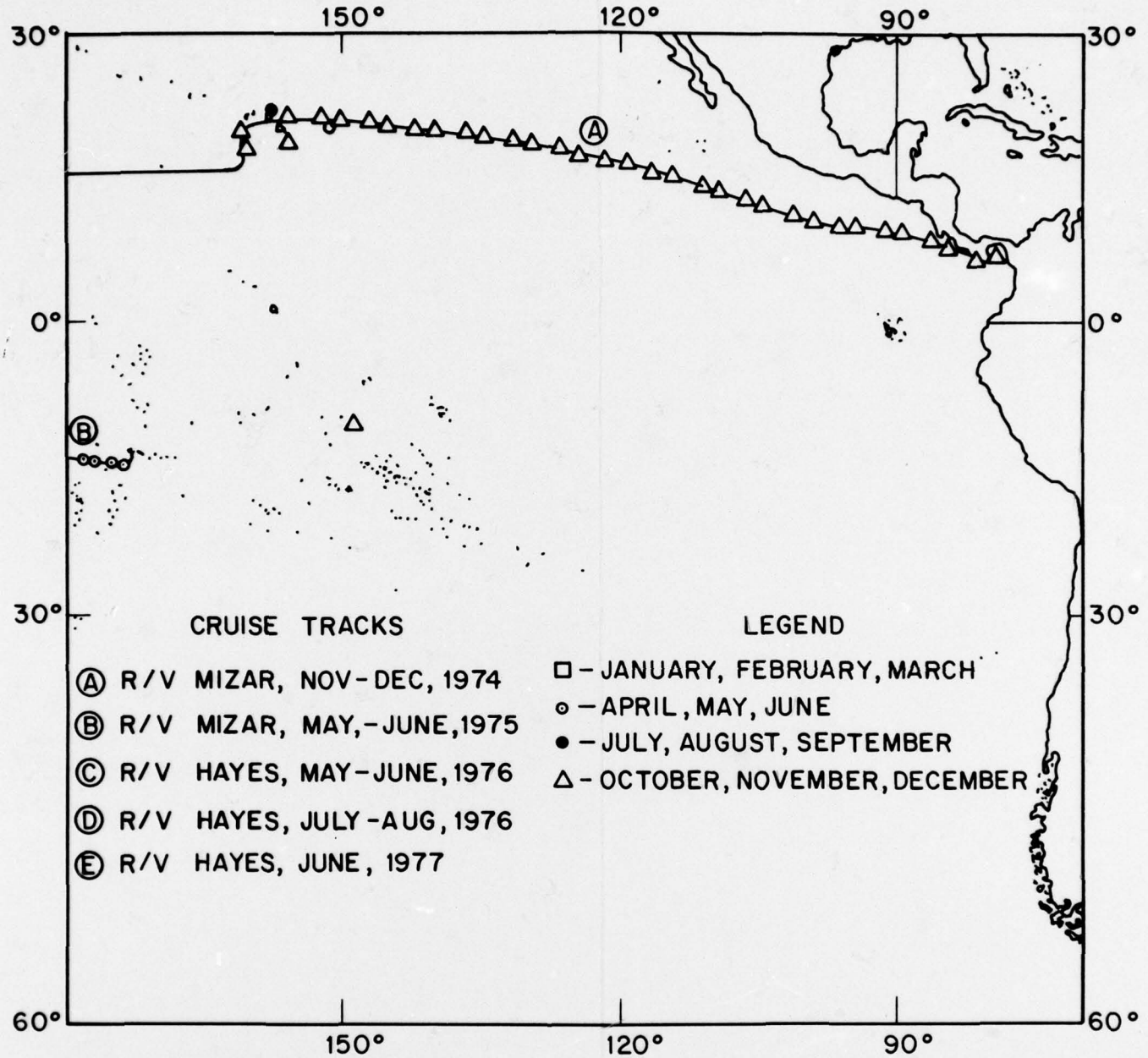


Fig. 10 — Seasonal distribution of bioluminescence in the east central and south Pacific Ocean

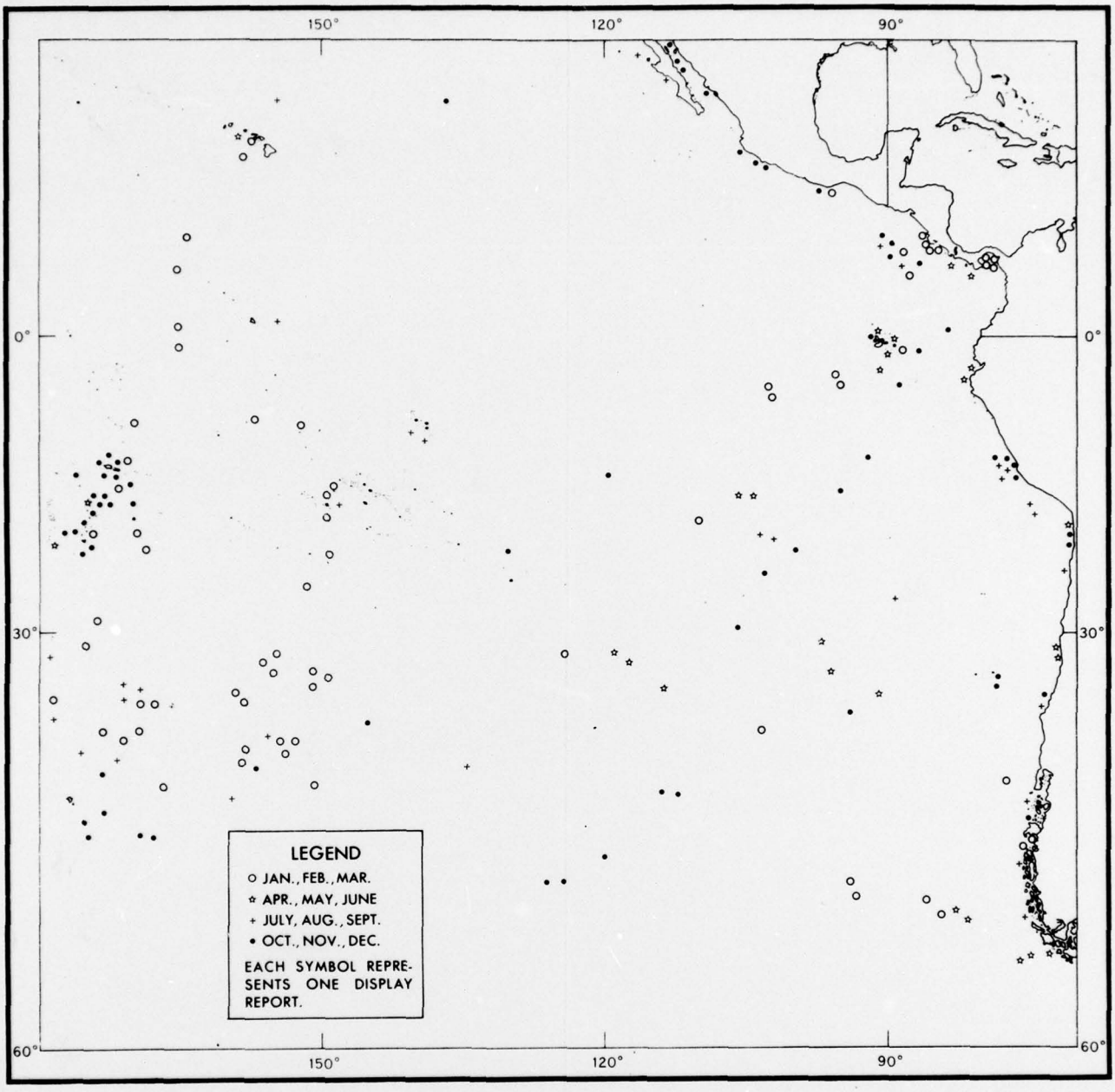


Fig. 11 — Seasonal distribution to bioluminescent displays in the east central and south Pacific Ocean (Staples, 1966)

(Page 38 Blank)

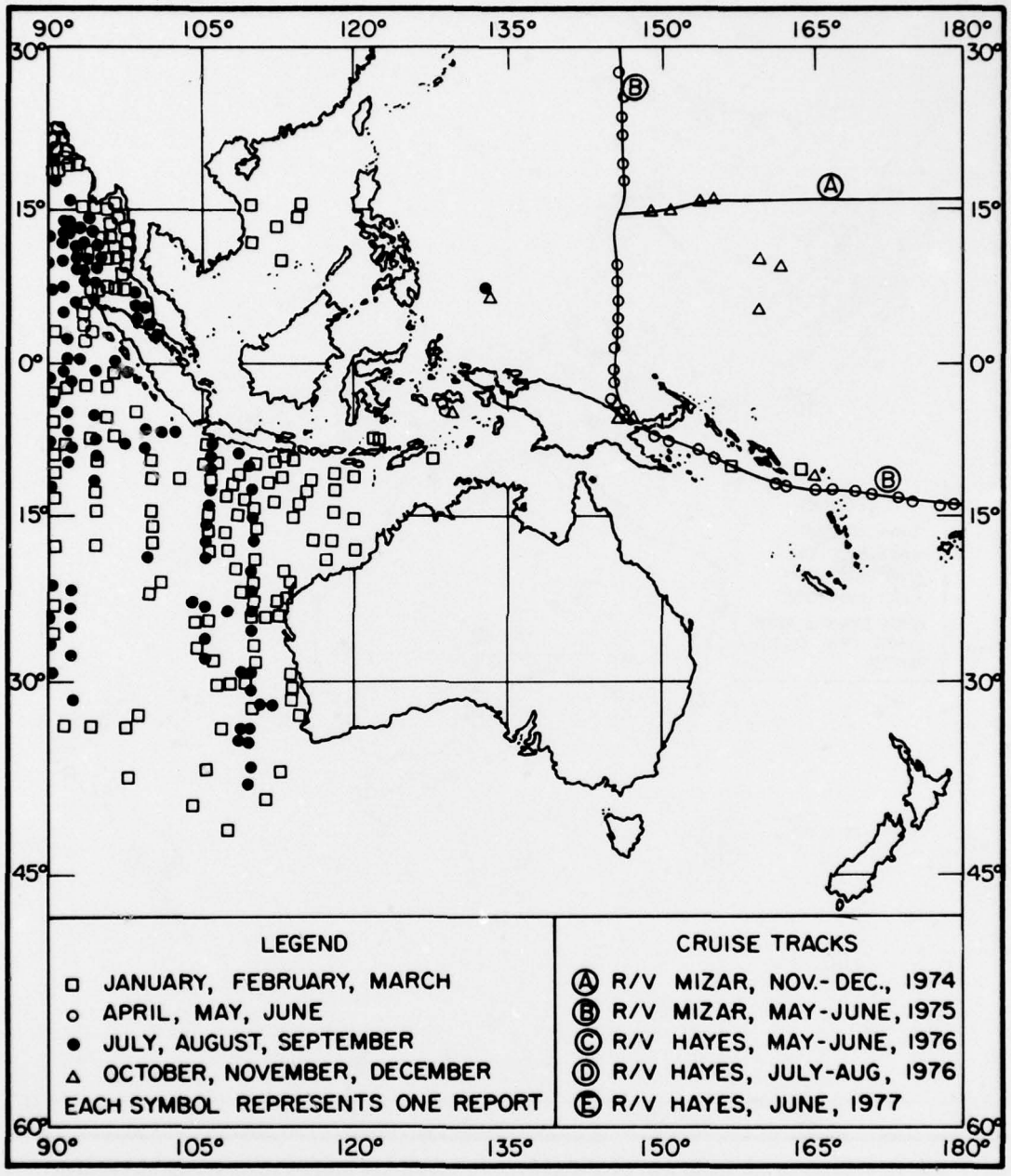


Fig. 12 — Seasonal distribution of bioluminescence in the western south Pacific and eastern Indian Oceans

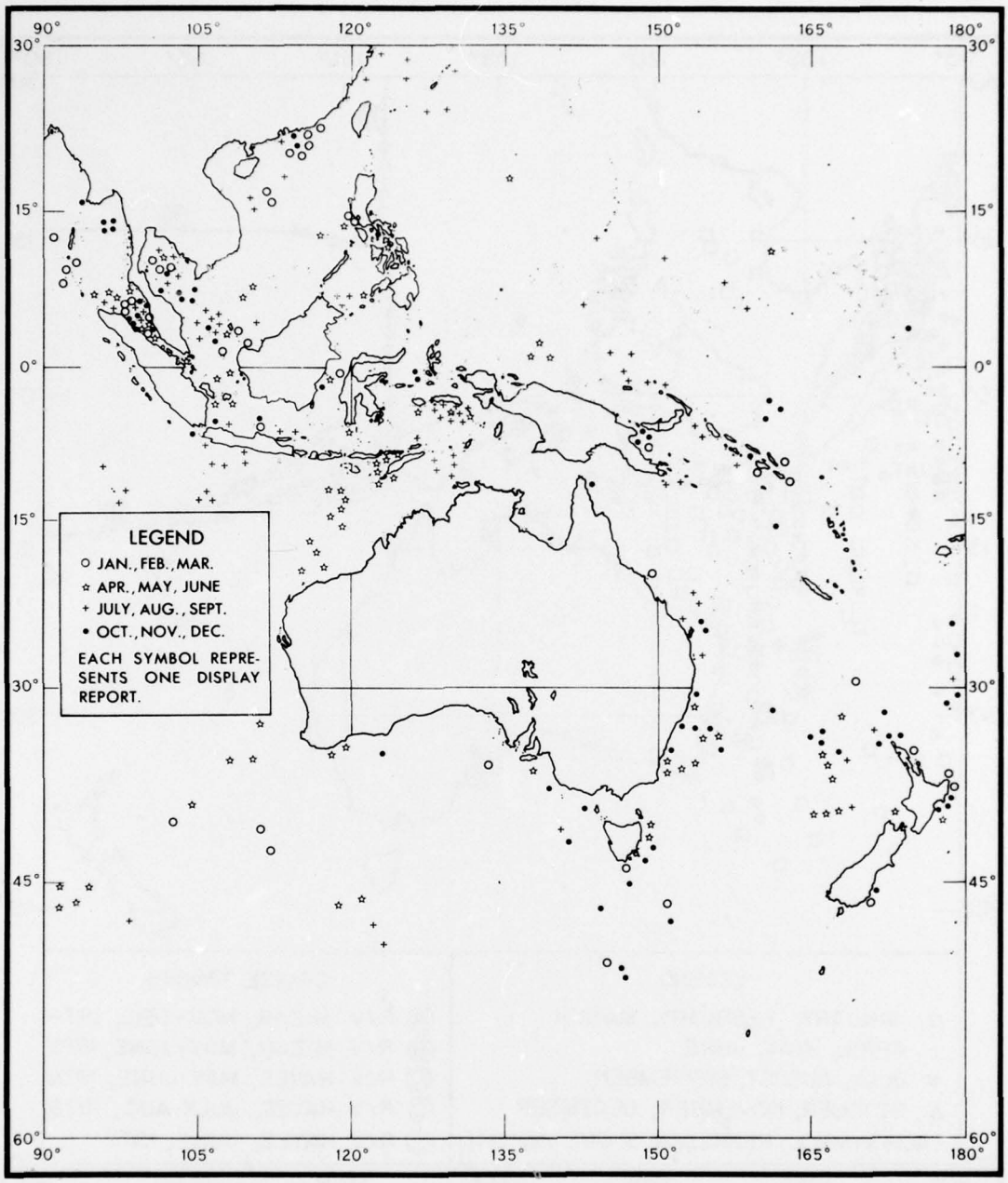
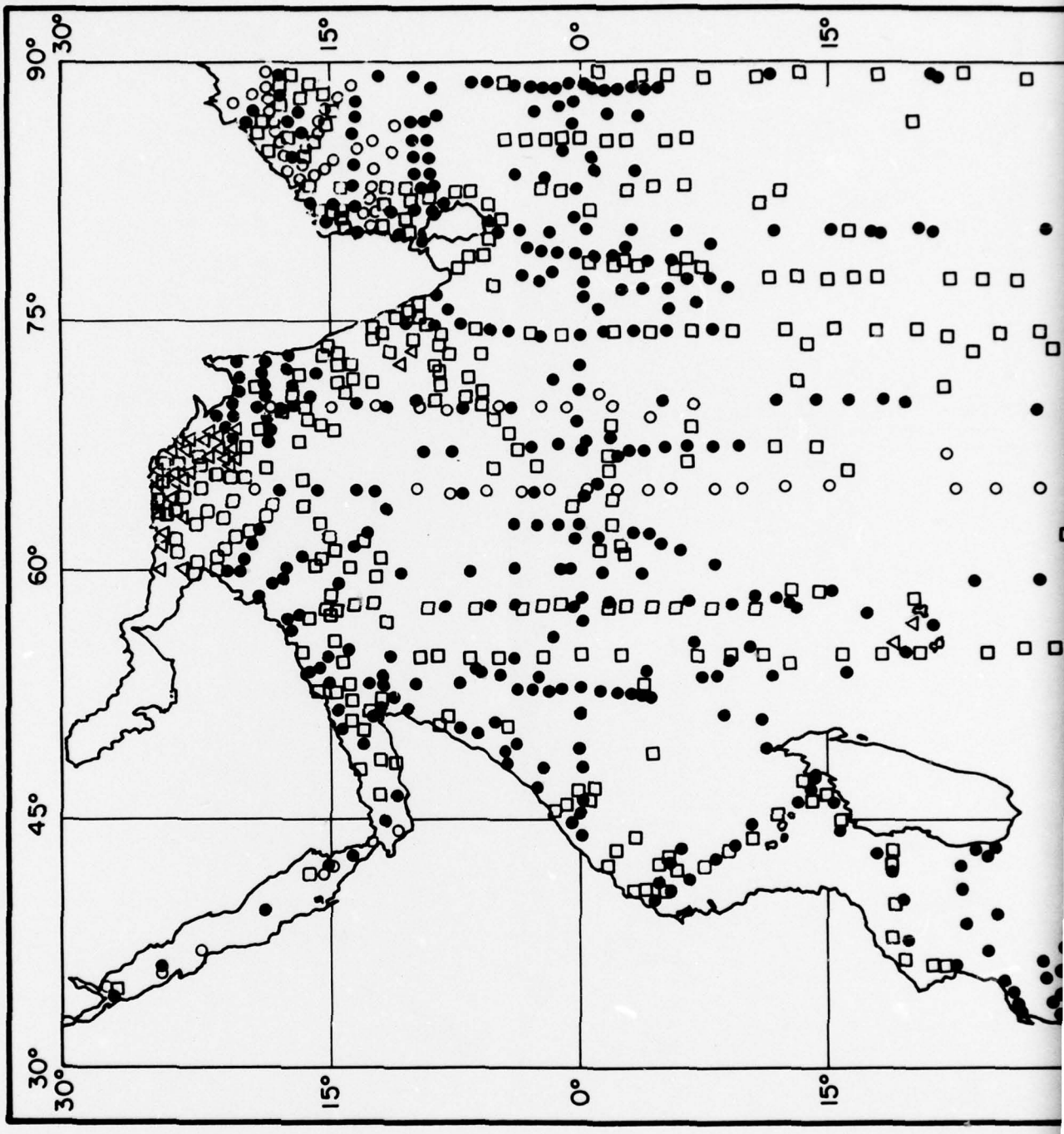


Fig. 13 — Seasonal distribution of bioluminescent displays in the western south Pacific and eastern Indian Oceans (Staples, 1966)


90°
75°
60°
45°
30°
30°
15°
0°
15°
30°
15°
0°
15°

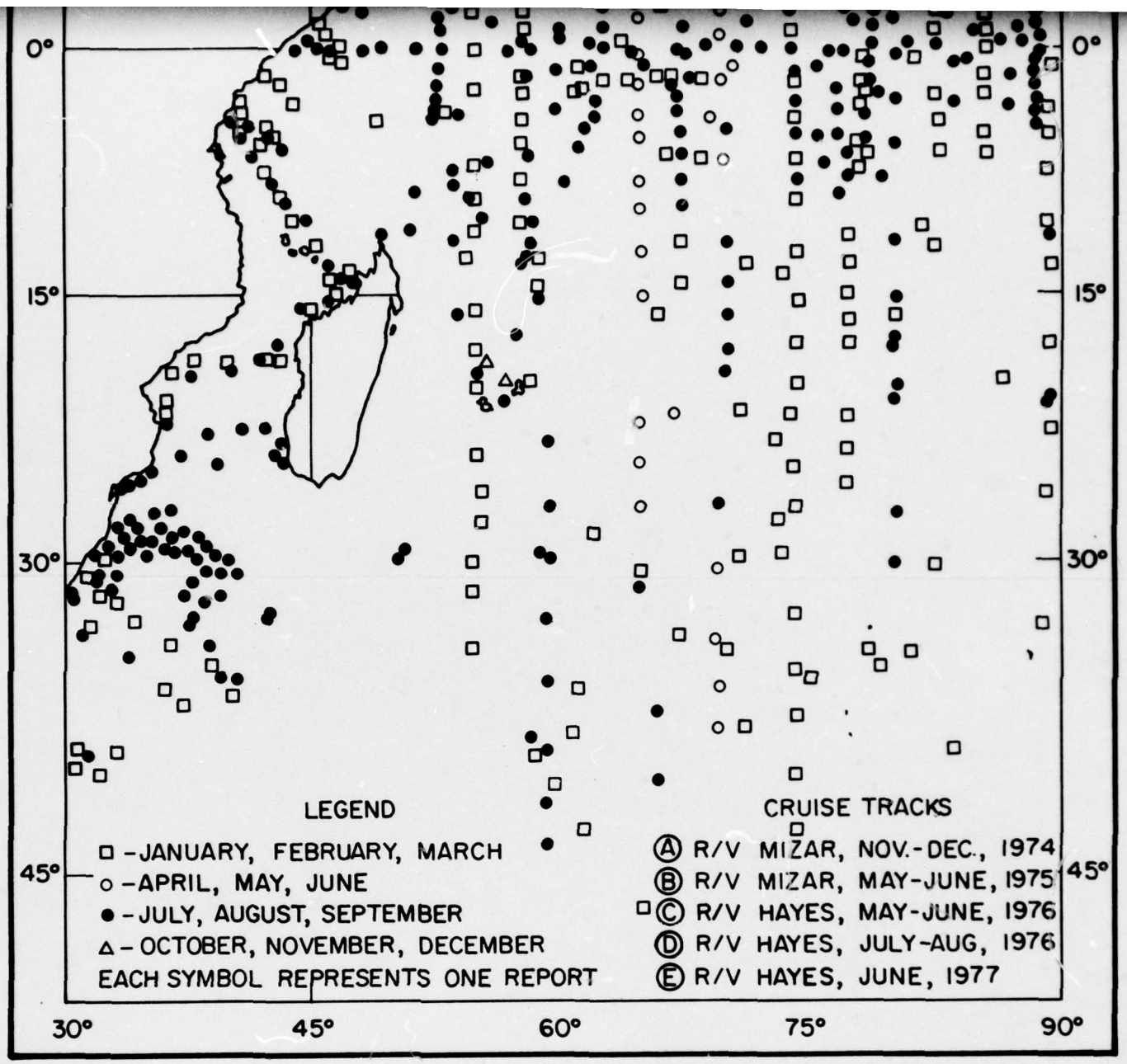
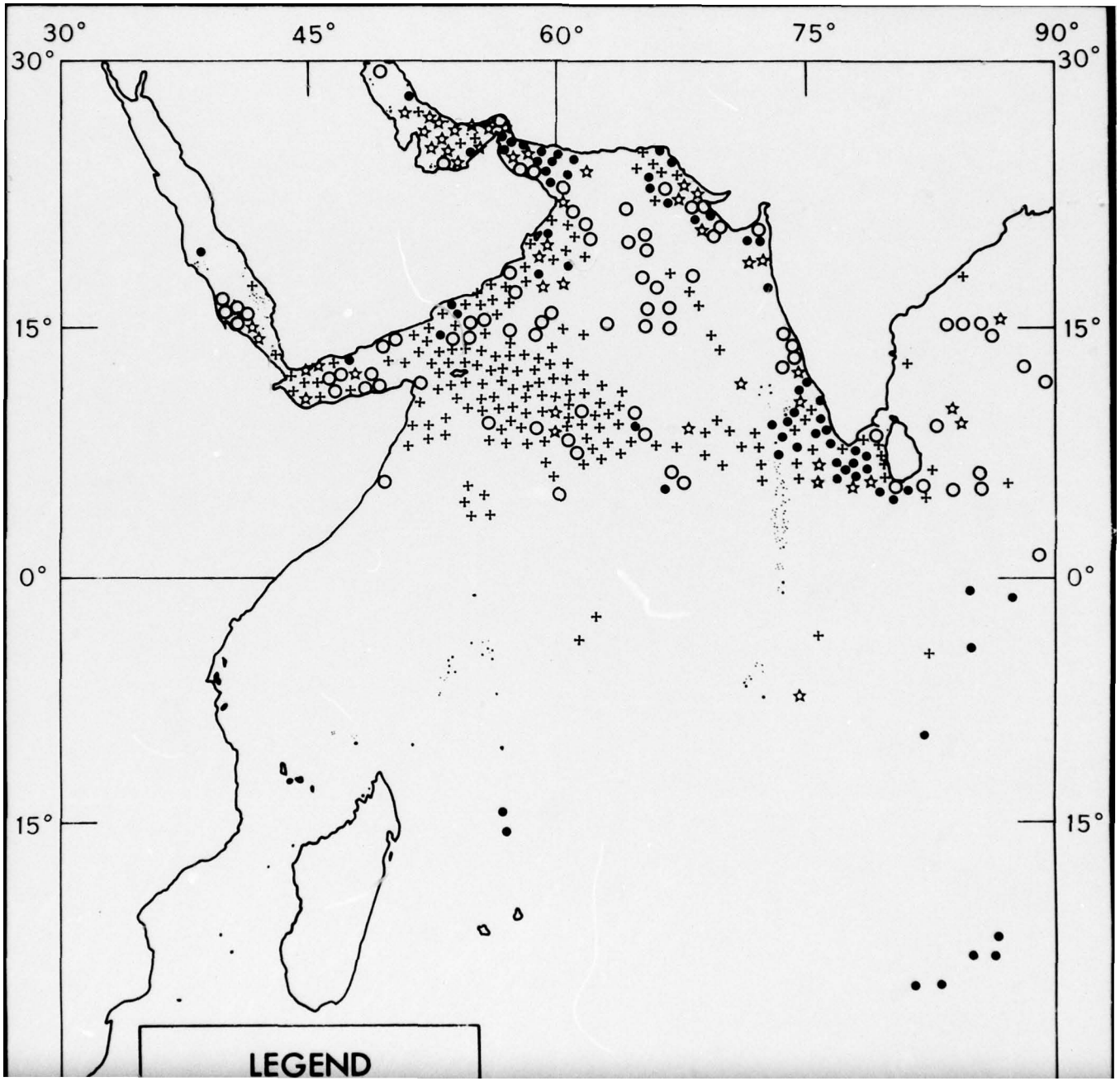
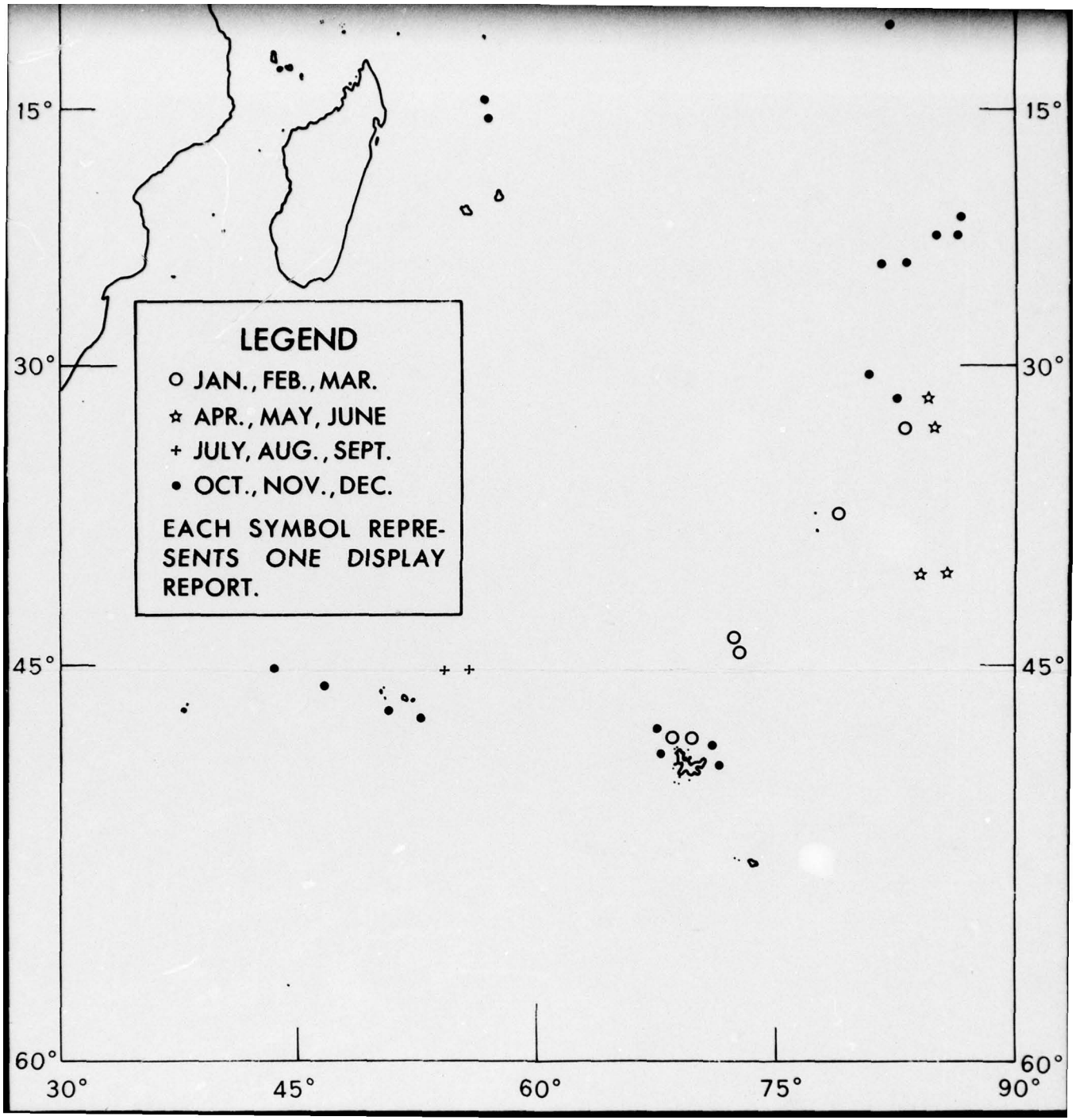


Fig. 14 — Seasonal distribution of bioluminescence in the central and western Indian Ocean and adjacent seas


30°
45°
60°
75°
90°
30°
15°
0°
15°
LEGEND


LEGEND
o JAN., FEB., MAR.
☆ APR., MAY, JUNE
+ JULY, AUG., SEPT.
• OCT., NOV., DEC.
EACH SYMBOL REPRESENTS ONE DISPLAY REPORT.
15°
30°
45°
60°
30°
45°
60°
75°
90°

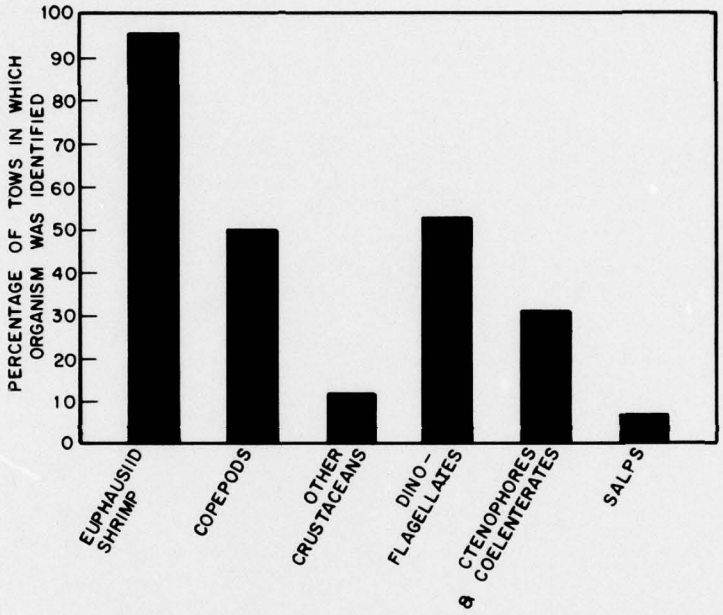


Fig. 16 — Frequency of occurrence of luminescent organisms in plankton tows on NRL cruises

*U.S. GOVERNMENT PRINTING OFFICE: 1978 261-250/0011 1-3